TERMS OF SERVICE: ENHANCING ESTABLISHMENT AND GROWTH OF INTERSEEDED COVER CROPS

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

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December 2017

ABSTRACT

Winter cover crops provide a suite of benefits but their use is limited because there is often not enough time after harvesting crops in the fall to establish cover crops before winter. Problems with establishment may be overcome by interseeding, where cover crops are seeded between rows of cash crops prior to harvest. Interseeded cover crops can provide greater ecosystem services than cover crops established after harvest, including erosion control and weed suppression. In addition to these services, interseeded cover crops might also provide habitat for invertebrate seed predators such as carabid beetles and crickets, which feed on weed seeds. We established a field experiment to investigate how cash crop planting density affects interseeded cover crop performance during the transition to certified organic production. We measured corn density, light transmission through the corn canopy, cover crop and weed biomass, and corn grain yield. We analyzed the relationship between these factors with regression, mixed models, path analysis, and partial correlation. The effect of corn density on interseeded cover crop biomass was significant when quantified both directly and indirectly as mediated by light transmission and weed biomass. At the October sample date, weed biomass was 31% lower in plots with interseeded cover crops than plots without, and corn grain yield was not different between plots with interseeded cover crops and plots without. We also conducted a laboratory experiment to explore the potential for cover crop seeds to be eaten by weed seed predators. Using four common invertebrate weed seed predators and a series of No Choice and Choice feeding assays, we presented seeds of ten cover crop species and three weed species to

individual carabid beetles and crickets. We analyzed No Choice preference with logistic regression and Choice with Vanderploeg and Scavia's electivity index and mixed models. We found that all four invertebrate seed predators consumed cover crop seeds and that preference varied by plant species and insect species. Overall results show that cover crop interseeding can be used to overcome one of the primary barriers to cover crop adoption and provide ecosystem services, but that cover crop seeds are susceptible to seed predation and thus cover crop species selection and seeding method are important to consider.

BIOGRAPHICAL SKETCH

Connor Youngerman grew up on a small farm on Prince Edward Island, Canada. He majored in biology at the University of Prince Edward Island and studied aquatic insects for his honors thesis. Before coming to Cornell, Connor lived in Arizona and worked as a ranch hand, veterinary technician and martial arts instructor. He later moved to Massachusetts and worked as a green roofer and organic farm manager.

ACKNOWLEDGMENTS

Unabashed gratitude to my advisors, Drs. Matt Ryan, Antonio DiTommaso and John Losey for their mentorship and guidance throughout the duration of my degree. I could not have done this without you. Additional thanks to Drs. William Curran and Steven Mirsky, and their field crews, for their collaboration and help. Many thanks to the members of the Sustainable Cropping Systems Lab, especially Chris Pelzer and Sandra Wayman. A special thank you to Stephen Parry at CSCU and Stephane Cordeau from INRA for their patience and instruction with statistics.

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PROLOGUE

The Green Revolution lifted the threat of starvation for hundreds of millions of people and changed the world. Biotechnology has boosted yields for industrial agriculture (Francis et al., 2017), but this model of food production is wholly dependent on the diminishing effects of synthetic inputs (Mortensen et al., 2012; Clements and DiTommaso, 2010). Proponents of this model argue for its expansion, and claim it is the only way to double food production to feed a projected 9 billion people by 2050 (Baenziger et al., 2017). However, recent work has shown this claim to be exaggerated (Hunter et al., 2017), even without addressing dietary shifts and food waste (Foley, 2013). Industrial agriculture is responsible for large-scale nitrate, phosphorus, pesticide and pathogen pollution in soil and water (Parris, 2011), and the global degradation and destruction of soil, natural habitats and biodiversity (Frison et al., 2016). Unexpected impacts to human health are also proving to be concomitant to the widespread use of pesticides (Wilson and Tisdell, 2001; Zhang et al., 2015). Arguably, the benefits of the Green Revolution are reaching a point of diminishing return; its sustainability should be seriously questioned. Reductionist science may increase food production, but not without global consequences. The future of agriculture should instead be based on a holistic model for sustainable food production (Holt-Gimenez and Alreri, 2012; Frison et al., 2016).

Organic agriculture could be the foundation for a sustainable food production system. Compared to conventional production, environmental advantages of organic agriculture include: improved soil health and structure, reduced fertilizer and pesticide

leaching, reduced greenhouse gas emissions, and increased biodiversity (Seufert and Ramankutty, 2017; Reganold and Wachter, 2016; Bengtsson et al., 2005). Previous research estimated that a countrywide transition to organic production in Canada would reduce national energy consumption by 0.8 %, greenhouse gas emissions by 0.6 %, and acidifying emissions by 1.0 % (Pelletier et al., 2008). Greater labor costs are associated with organic production, but higher market premiums translate to greater profitability compared to conventional production (Crowder and Reganold, 2015). Sociologically, organic production cements small farmers as key actors for regional food security (Altieri, 2009), by empowering them to run diverse operations and sell their produce directly and locally to consumers (Hall et al., 2001). Given its multi-dimensional benefits, organic agriculture should be a large sector of global agriculture. As of 2012, only about 0.7 % of all US farms were under organic management (National Sustainable Agriculture Coalition, 2014).

What is stopping farmers from transitioning to organic production? Part of the problem is lack of funding and misinformation about organic agriculture. Delonge et al., (2016) found only about 10 % of the 2014 USDA Research, Extension and Economics budget went to projects related to sustainable agriculture or agroecology, including organic production. The majority of funded projects focused on enhancing yields, rather than systems-based research (Delonge et al., 2016). The yield gap between conventional and organic production is often debated (e.g., Trewaves, 2001; Seufert and Ramankutty, 2012; Sacco et al., 2015; Seufert and Ramankutty, 2017; Frison et al., 2016; Bedoussac et al., 2015). Agribusiness endorses the view of low

organic yields through public relations campaigns targeted at farmers and scientific societies to delegitimize criticisms of their products (Hodai and Graves, 2012). The coupling of poor funding and misinformation is a potent synergism to impede the dissemination of organic agriculture research to farmers.

Farmers are generally cautious about transitioning to organic production, because many are financially "locked-in" to conventional farming (Wilson and Tisdell, 2001). In general, low yields are a hallmark of the transition period (Drinkwater et al., 1995; Caldwell et al., 2014), and the market for transitional grain is not as lucrative as for organic grain (Menalled et al., 2009). Loss from lower yields and grain prices, coupled with new weed management requirements during the transition to organic production are not economically feasible for many farmers. However, expert management and diversified cropping systems in the transition period may facilitate higher yields (Martini et al., 2004; Ponisio et al., 2014). Moreover, yields increase after the transition to organic is complete (Delate and Cambardella, 2004).

Weeds can cause a significant reduction to yield (Cousens, 1985). No weed control tactics are as effective and reliable as synthetic herbicides (Bastiaans et al., 2008), and thus organic farmers often rely on "many little hammers approach" to reduce weed problems (Liebman and Gallandt, 1997). Crop rotations, intercropping, altering crop population density, and tillage are effective weed management tools (Liebman and Dyck, 1993; Tollenaar et al., 1994; Schipanski et al., 2014a). The learning curve for these cultural methods can be steep (Menalled, 2009). But, if these

methods are properly implemented they are an effective system for weed management (Smith et al., 2009).

Farmers who want to change to a more sustainable and lucrative organic production must first navigate the 36-month transition period. If the transition period can be made less financially burdensome, it is likely that more farmers will switch to organic production. Because corn is often the most profitable crop that farmers grow, the ability to grow corn during the transition to organic production could facilitate widespread adoption of organic production. However, in order to grow corn successfully during the transition to organic production, weeds must be suppressed and adequate soil nutrients must be available to the crop to produce acceptable yields.

The goal of this research was to test the effects of interseeded cover crops in corn during the transition to certified organic production. A field experiment was conducted at New York, Pennsylvania, and Maryland in 2016. In Chapter 1, the effects of corn density on interseeded cover crop performance, weed biomass, and corn yield are reported. Laboratory research was conducted to compare several species of cover crops and weeds in terms of seed predator preference, and is presented in Chapter 2.

CHAPTER 1

THE EFFECTS OF CORN PLANTING DENSITY ON INTERSEEDED COVER CROPS, WEEDS, AND CORN GRAIN YIELD

ABSTRACT

Cover crops can provide a suite of ecosystem services and increase the sustainability of cropping systems. In 2016, we drill interseeded cover crops into corn that was planted across a range of densities and measured corn density, cover crop biomass, weed biomass, and corn grain yield. The relationship between these variables was analyzed with regression and path analysis. We hypothesized that 1) light transmission, cover crop biomass, and weed biomass would decrease as corn planting density increased; 2) the effect of corn planting density on cover crop biomass would be mediated by light transmission and weed biomass; 3) weed biomass would decrease as cover crop biomass increased. We observed a tradeoff between corn density and cover crop biomass. Path analysis showed a direct and indirect effect of corn density on interseeded cover crop biomass. At the October sample date, weed biomass was 31% lower in plots with interseeded cover crops than plots without. No difference in corn grain yield was observed between treatments with and without cover crops. These results suggest that farmers can increase the performance of interseeded cover crops by using corn planting rates that are slightly lower than what is typically used without reducing corn grain yield. Additional research should be conducted to determine corn planting rate recommendations for maximizing both corn yield and cover crop biomass across a wider range of environments.

INTRODUCTION

Cover crops are a potential agroecological tool to integrate into a corn production system. The Soil Science Society of America defines cover crops as "close-growing crops, which provide soil protection, seeding protection, and soil improvement between periods of normal crop production […]" (SSSA, 2008). Cover crops are promoted by agricultural companies to help farmers save money and build soil health after the primary crop has been harvested (Monsanto, 2015; Syngenta, 2017). These statements undersell the potential and applicability of cover crops. As Schipanski et al., (2014b) point out, "The most common metrics for evaluating cropping systems are grain and forage yields and short-term profitability. Within this context, cover crops are treated as a tool to be used only if they do not interfere with cash crop production." This narrative has largely driven cover crop research, which typically evaluates cover crop use before or after corn production (e.g., Gabriel and Quemada, 2011; Krueger et al., 2011; Parr et al., 2011). A more appropriate definition of cover crops is "a plant that is used primarily to slow erosion, improve soil health, enhance water availability, smother weeds, help control pests and diseases [and] increase biodiversity […] (SARE, 2012). Schipanski et al., (2014b) and Blanco-Canqui et al., (2015) provide excellent reviews of these ecosystem services.

The magnitude and variability of ecosystem services provided by cover crops may depend on cover crop species selection and management practices such as planting date and termination date (Smith et al., 2014; Lawson et al., 2015). In

general, most ecosystem services are correlated with increased cover crop biomass. These services include weed suppression (Pullaro et al., 2006), pollinator abundance (Ellis and Barbarchek, 2015), earthworm abundance (Blanco-Canqui et al., 2011), reduced phosphorus loading (Kleinman et al., 2005), improved soil health (Abawi and Widmer, 2000), increased soil organic matter (Finney et al., 2016), and reduced soil erosion (Kaspar et al., 2001). The latter three services are the most common reasons that farmers choose to grow cover crops (Wayman et al., 2016), but overall, very few farmers actually use cover crops.

A recent Census of Agriculture found a paucity of cover crop use by US farmers, with only 3-7% capitalizing on cover crop services (SARE et al, 2015). Farmers in drier regions of the country have good reason not to use cover crops, because cover crops reduce soil moisture and can lower subsequent yields (Nielsen et al., 2016). But why are so few farmers in the rest of the country growing cover crops? According to a 2014 survey of 2814 US farmers, 21% reported problems with establishment and 18% reported the time and labor needed for management as the main reasons to not grow cover crops (SARE, 2014). These obstacles are symptomatic of the narrative presented by SSSA (2008) and Schipanski et al. (2014b), where cover crops are grown between periods of cash crop cultivation. Within this context, it is difficult to establish cover crops. For example, if a corn farmer harvests in November, the window to plant cover crops is narrow and may compete with other vital field operations (Roesch-McNally et al., 2017). A similar problem may arise in spring when cover crops need to be fully terminated before planting. Such constraints make it

understandable that the majority of farmers do not plant cover crops, but these constraints are not definitive. Interseeding is a method used to plant cover crops that can help overcome these obstacles.

Interseeding is a form of relay intercropping where cover crops are planted while the primary crop is still growing. Early establishment of interseeded cover crops directly translates into an increased cover crop biomass, N uptake, and reduced potential for nitrate leaching over the winter (Hashemi et al., 2010; Feyereisen et al., 2006, Staver and Brinsfield, 1998). Another major benefit of establishing cover crops early with interseeding is that legumes and other species that require longer periods to establish before winter can be used. In corn, interseeding is generally accomplished by aerial or ground broadcasting, which means placing cover crop seeds directly on the soil surface without incorporating them. However, broadcasting does not guarantee good seed placement and establishment (Hively and Cox, 2001), as seeds can get stuck in the canopy of the cash crop (Baker and Griffis, 2009), be blown away, or transported out of the field with surface water flow (Fisher et al., 2011). These methods are most successful when field conditions are moist and the soil is friable. The advantage to broadcasting, specifically aerial broadcasting, is that it is possible to accomplish when fields are too wet for heavy machinery (NRCS Iowa, 2010). If conditions are too dry however, there is a danger that broadcast seeds will desiccate beyond germinability (Baker and Griffis, 2009).

These problems with broadcasting can be overcome by using a high clearance drill interseeder to plant cover crops (Shipman, 2010). Similar to standard grain drills,

high clearance drill interseeders plant cover crop seeds into a seed furrow between rows of cash crops that are actively growing. Advantages of drill interseeding compared to broadcast seeding are twofold: 1) it ensures seed-to-soil contact so seeds are buffered from wind and desiccation; 2) cover crops are seeded uniformly at a specific seeding rate. High clearance interseeders allow better placement of seeds (Shipman, 2010), and lay them in straight rows between the rows of cash crops. In previous research, Fisher et al. (2011) found drilled cover crops had up to 10 times greater seedling emergence per m^2 than broadcast cover crops, depending on site and sample date.

Although drill interseeding cover crops can overcome many of the challenges that limit cover crop adoption, management of the host cash crop can greatly affect cover crop establishment and performance. For example, residual herbicides that are commonly used to control weeds in corn, such as atrazine, have extended plant back restrictions and can be problematic for cover crop establishment (Curran and Lingenfelter, 2012). In organic cropping systems, farmers often plant cash crops at relatively high planting rates to hasten canopy closure and enhance weed suppression (Bond and Grundy 2001; Bastiaans et al., 2008). Even with increased seed costs, high cash crop planting rates can be more profitable if the enhanced weed suppression leads to increased crop yields (Liebert et al., 2017). On the other hand, increasing shading can also reduce the establishment and growth of interseeded cover crops.

The aim of this experiment was to determine the effect of corn planting density on drill interseeded cover crop performance, weed suppression, and corn grain yield during the transition to certified organic production. The relationship between these variables was analyzed with regression and path analysis. We hypothesized that 1) light transmission, and cover crop and weed biomass would decrease as corn planting density increased; 2) the effect of corn planting density on cover crop biomass would be mediated by light transmission and weed biomass; 3) weed biomass would be suppressed by interseeded cover crops.

MATERIALS AND METHODS

Site Descriptions

This experiment was conducted in 2016 at three locations in the northeastern United States. The first site was at the Cornell Musgrave Research Farm near Aurora, NY (42.73°N, 76.65°W). The soil type at this site was 82.8% Lima silt loam, (fine-loamy Oxyaquic Hapludalf) with 0 to 3% slopes, and 17.2% Kendaia and Lyons soils (mesic Aeric Endoaquepts / mesic Mollic Endoaquepts) with 0 to 3% slopes. The previous crop at this site were cover crops on the eastern half and summer forage crops on the western half. The second site was at the Penn State Russell E. Larson Agricultural Research Center near Pennsylvania Furnace, PA (40.73°N, 77.93°W). The soil type at this site was 24.7% Hagerstown silt loam (mesic Typic Hapludalfs) with 3-8% slopes, 15% Hagerstown silty clay loam with 3-8% slopes, 36.1% Hagerstown silty clay loam with 8-15% slopes, and Openquon-Hagerstown complex (mesic Lithic Hapludalfs) with 3-8% slopes. The previous crop at this site was organic soybean. The third site was at the USDA Beltsville Agricultural Research Center in Beltsville, MD (39.03°N, 76.93W°). The soil type at this site was 100% Codorus and Hatboro soils (mesic Fluvaquentic Endoaquepts/Dystrudepts), with 0% slope and frequent flooding. The previous crop at this site was organic soybean. Fields at each site were managed using organic production methods for the duration of the experiment.

Experimental Design

The experiment was arranged as a randomized complete block design with four replication blocks at each site. At all sites, each block had five treatment plots that measured 12 m x 14 m. Blocks were spaced 12 m from each other. Five treatments were compared in each block: 1) 'No Corn' (no corn was planted; interseeded cover crops were planted); 2) 'Low' (corn planting density of 37,050 plants ha^{-1}; interseeded cover crops were planted); 3) 'Medium' (corn planting density of 74,100 plants ha^{-1}; interseeded cover crops were planted); 4) 'High' (corn planting density of 111,150 plants ha^{-1}; interseeded cover crops were planted); 5) 'Medium Control' (corn planting density of 74,100 plants ha^{-1}; no interseeded cover crops were planted).

Field Operations

In late spring 2016, organic fertilizer was applied at each site prior to tillage to ensure adequate corn growth (Table 1.1). Poultry manure (5-4-3, Kreher's Farm Fresh Eggs, Clarence, NY) was used in New York at a rate of 280 kg ha^{-1}. Dairy manure was used in PA at a rate of 51,447 L ha^{-1} and supplemented with Chilean nitrate (16-0-0) at a rate of 224 kg ha^{-1}. Poultry manure (3-2-3, Purdue Agricycle LLC, Seaford, DE) was used in Maryland at a rate of 280 kg ha^{-1}. Experimental fields were plowed and disked after fertilizer application, and cultimulched immediately before planting (Table 1.1).

Untreated conventional corn seed (*Zea mays* L.; cv. 'Viking 69-99' 99 day relative maturity) was planted in late May at all sites (Table 1.1). This variety is marketed as a flex ear type that can grow multiple ears if conditions are favorable.

Corn was planted with a 4-row, 3 m wide planter (76 cm rows) at each site. A total of 16 rows was planted in each treatment. All blocks were planted on the same day at each site. Row length was greater than 14 m to provide extra seedlings if transplanting was needed to fill in gaps. Planters were calibrated to specific planting rates (37,050 plants ha^{-1}, 74,100 plants ha^{-1}, 111,150 plants ha^{-1}) and a test run was conducted after each new calibration to verify seed planting rate. Seeds were dug up at the end of each row to verify no planter malfunctions were occurring. Seedling spacing was verified after emergence. Any gaps in the corn rows greater than 1 m were replanted to appropriate densities. Replanting was necessary in New York and was done by transplanting seedlings from the ends of the corn rows. Transplanted seedlings had a root ball volume of approximately 4 L and were watered with 2 L of water after transplanting. A smaller amount of replanting was also necessary in Pennsylvania and was done by direct sowing.

Four weed management cultivation practices were used in New York and Pennsylvania, and three weed management cultivation practices were used in Maryland (Table 1.1). A tine weeder was used for two blind cultivation events in New York and Pennsylvania, one before and one after the corn had emerged. Only the first blind cultivation event occurred in Maryland. The tine weeder was tested prior to the second blind cultivation to ensure its pressure was aggressive enough to uproot weeds without damaging corn seedlings. An S-tine cultivator was used to complete two inter-row cultivations events at each site. One inter-row cultivation occurred when the corn was at the V2-V3 stage, the other occurred when the corn was at the V4-V5 stage.

Once the corn reached its V5 growth stage, it was interseeded with a cover crop mixture. Dave Wilson, Research Agronomist at King's AgriSeeds Inc. in Ronks, PA provided the mixture, which was used at all sites. The mixture was seeded at 66 kg ha^{-1}, and contained 51% (by weight) winter cereal rye (*Secale cereal* L.), 25% annual ryegrass (*Lolium multiflorum* L.), 14% hairy vetch (*Vicia villosa* R.), and 10% red clover (*Trifolium pratense* L.). The cover crop was interseeded into the corn with a high-clearance drill interseeder (InterSeeder Technologies, Woodward, PA) at each site. Cover crop seeds were inoculated with the appropriate *Rhizobium leguminosarum* strains immediately prior to seeding.

The Pennsylvania site was irrigated on August 1 due to extreme drought conditions (Table 1.3). A total of 2.5 cm of water was applied to the entire field on this date. Irrigation was not used at the other two sites.

Sampling

Emerged corn density was assessed in each treatment. The number of corn plants per 7.6 m row length in rows 6, 7, 10 and 11 of each treatment was counted (Figure 1.1). The number of plants per 7.6 m row length was converted to plants m^{-2} units for analysis.

Photosynthetically active radiation (PAR) was measured with a line quantum sensor (LI-190, Li-Cor, Inc., Lincoln, NE), point sensor (LI-191, Li-Cor, Inc., Lincoln, NE), and data logger (LI-1400, Li-Cor, Inc., Lincoln, NE) to determine light transmission through the corn canopy. There were two PAR measurement dates at

each site, one immediately preceding cover crop interseeding and the other immediately preceding the first cover crop biomass collection. PAR was measured at four locations in each treatment (Figure 1.1). In previous research, four unique PAR locations provided a reliable estimate of PAR for a whole corn field (Singer et al., 2011). PAR measurements were taken between 10 am and 2 pm under minimal cloud cover. The point sensor was held level directly above the corn canopy and line quantum sensor was held level on the soil surface. Three measurements were taken at each location with two "blank" measurements between locations, five between each treatment, and ten between each block. Field notes detailed the order of PAR measurements to ensure the data matched their respective locations. Due to time constraints, PAR in Maryland was only sampled at two locations in each treatment.

Weed biomass and cover crop biomass were sampled approximately 50 and 110 days after cover crop interseeding (Table 1.1). At each date, biomass was sampled from within two, 0.5 m^2 quadrats per treatment (Figure 1.1). Quadrats "A" and "D" were sampled approximately 50 days after interseeding; quadrats "B" and "C" were sampled approximately 110 days after interseeding. All three rows of interseeded cover crops were sampled along a 65 cm length (Figure 1.2). Cover crops were cut at ground level with scissors and placed into an appropriately labeled paper bag. All weeds greater than 2.5 cm were collected from the 0.5 m^2 quadrat and were cut at ground level with field scissors, and packed into an appropriately labeled paper bag. After sampling, all biomass was oven dried at 60°C for two weeks, then weighed. Biomass weights were converted to g m^{-2} units for analysis.

Grain yield was collected from the center 7.6 m of rows 6, 7, 10 and 11 in each treatment using a plot combine (Figure 1.1). Grain weight and moisture content were recorded by the harvester for each row pair and an adjusted weight at 15.5% moisture was calculated. Yield data were converted to g m^{-2} for analysis.

Table 1.1. Calendar of field operations and sampling events in 2016: Photosynthetically active radiation (PAR) 1 & 2 are the sample dates for measuring PAR, Biomass 1 & 2 are the sample dates for collecting cover crop and weed biomass, Corn density is when individual corn plants were counted.

Activity	New York	Pennsylvania	Maryland
Fertilizer application	May 11	May 18	May 24
Moldboard plowing & disking	May 12	May 18	May 25
Corn planting	May 12	May 27	May 26
Blind cultivation 1	May 25	May 31	May 27
Blind cultivation 2	Jun. 2	Jun. 10	–
Corn transplanting	Jun. 3	Jun. 10	–
Inter-row cultivation 1	Jun. 16	Jun. 21	Jun. 6
Inter-row cultivation 2	Jun. 21	Jul. 1	Jun. 27
Interseeding	Jun. 22	Jul. 1	Jun. 27
Irrigation	–§	Aug. 1	–
PAR 1	Jun. 21	Jun. 31	Jun. 27
PAR 2	Aug. 9	Aug. 12	Aug. 15
Biomass 1	Aug. 10	Aug. 12	Aug. 15
Biomass 2	Oct. 12	Nov. 11	Oct. 20
Corn density	Nov. 14	Nov. 15	Aug. 31
Corn harvest	Nov. 15	Nov. 15	Nov. 2

§ Dash indicates that operation or sampling event did not occur.

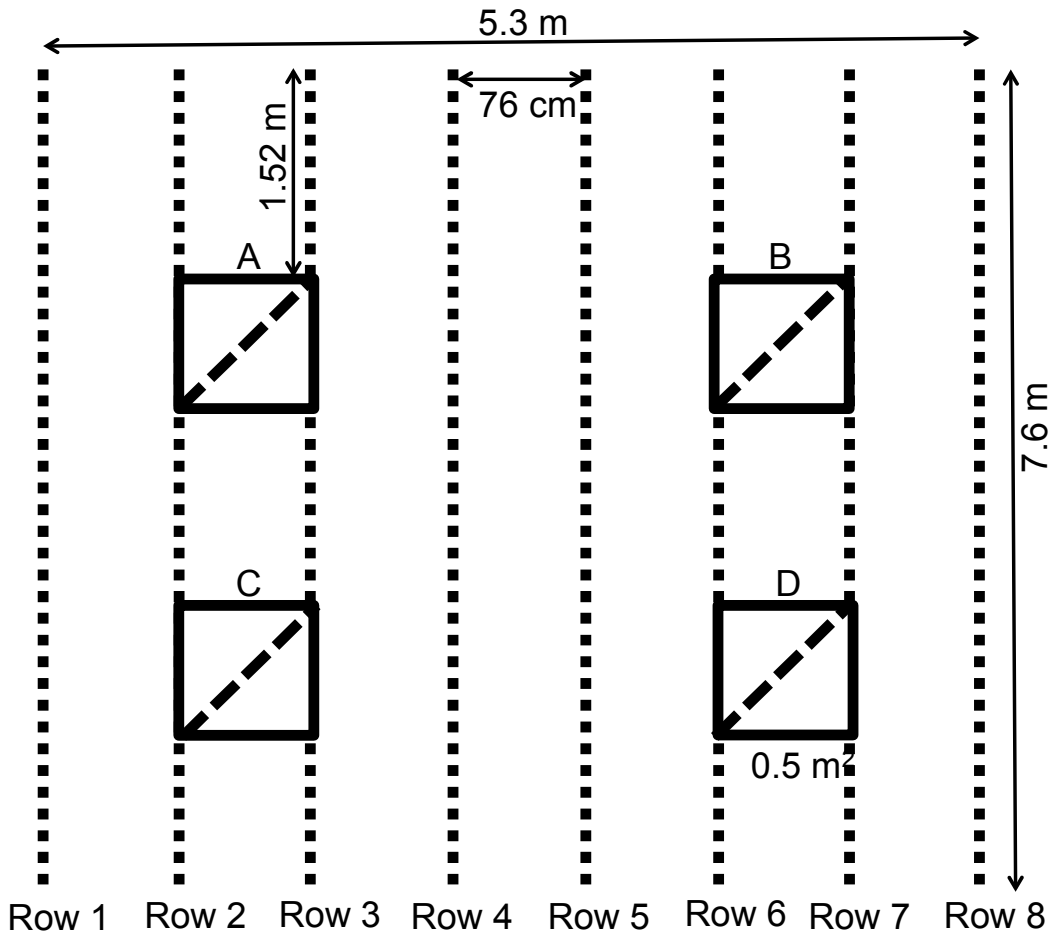

Figure 1.1. Sampling schematic of an experimental treatment: Vertical dotted lines represent corn rows, diagonal dashed lines represent PAR measurement locations, solid lined squares represent quadrats from which biomass was collected.

Statistical Analyses

All analyses were done with R version 3.2.2 (R Core Team, 2015). Five analyses were conducted to evaluate: 1) the effect of site, corn planting rate, and sample date on measured corn density, light transmission, weed biomass, cover crop biomass, and corn grain yield; 2) the linear relationships between measured corn density and light transmission, weed biomass, and cover crop biomass; 3) the direct

and indirect effects of measured corn density, light transmission and weed biomass on cover crop biomass; 4) the non-linear relationship between measured corn density and corn grain yield in plots with interseeded cover crops; 5) the effect of interseeded cover crops on weed biomass and corn grain yield. All biomass data were log-transformed, using the natural log plus 1 to deal with zeros in the data [ln(x + 1)], to satisfy assumptions of residual normality and equal variance.

Linear mixed effect models (packages lme4 and lmerTest) with block as a random effect were used to test for differences across sites, treatments, and sample times. Site and corn seeding rate (treatment) were fixed effects for all models; sample date was also used as a fixed effect for cover crop and weed biomass models. Data used for this analysis were from 'No Corn', 'Low', 'Medium', and 'High' treatments. ANOVAs were used to determine if fixed effects were significant. LSmeans (package lsmeans) was used to determine the difference in mean cover crop biomass, weed biomass, yield, and light transmission; significant differences of means ($P \leq 0.05$) were determined using Tukey's adjustment.

Linear regression was used to test the relationship between measured corn density and light transmission, weed biomass, and cover crop biomass within each site. Data used for these regression analyses were from 'No Corn', 'Low', 'Medium', and 'High' treatments.

Linear regression cannot describe the inter-relationship between all the measured response variables and corn planting density. Path analysis is therefore needed to analyze this network of causal relationships (Lefcheck, 2016). Path analysis

is a type of structural equation modeling (SEM) which facilitates the assessment networks of linear models (Sanchez, 2013). While path analysis was developed for social sciences, it is becoming a common statistical tool in agriculture and ecology (e.g., Quinio et al., 2017; Fu et al., 2015; Ryan et al., 2011). The advantage to using path analysis instead of multiple regression and partial correlation analysis is that path analysis incorporates mediating effects of model variables (Grace and Bollen, 2005).

The lavaan package was used for the path analysis. Only data from 'No Corn', 'Low', 'Medium', and 'High' treatments at the August sample date were used. Data from all sites were pooled for the path analysis. Data were standardized using:

$$\text{Standardized variable} = \frac{X_i - \overline{X}}{S_X}$$

where X*i* is the i^{th} observation, $\overline{X}$ is the mean of the variable, and S*x* is the standard deviation of the variable. This method allows the relationships between variables to be expressed as changes in standard deviation units, and makes it possible for direct comparisons across paths (Grace and Bollen, 2005).

Partial and semipartial R^2 values were calculated with the spcor and pcor functions (package ppcor) to assess the proportion of variance in cover crop biomass that was explained by corn density, light transmission, and weed biomass. This analysis was done to compliment the results of the path analysis. Data used for partial and semipartial correlation were from August sample dates in 'No Corn', 'Low', 'Medium', and 'High' treatments.

Multicolinearity of the predictor variables can be quantified with the *vif* function (package car) which calculates the variance inflation factor (VIF) for each predictor as: $VIF_i = \frac{1}{1-R_i^2}$ where R^2 is the multiple correlation coefficient of a predictor variable regressed on the remaining predictor variables (Belsley et al., 1980). A predictor variable that is uncorrelated to any other predictor variable will yield a VIF_i of 1 (Fox and Monette, 1992). Severe multicollinearity is evident when VIF > 10 (Kutner et al., 2005).

Determining which predictor variable, corn density, light transmission, or weed biomass explained the greatest variance of cover crop biomass is possible by comparing R^2 from their respective simple linear regressions (Table 1.5). This approach could be misleading however, because it does not evaluate the redundancy that exists between the predictors (Liebert et al., 2017). To determine the proportion of variance in cover crop biomass accounted for the predictor variables, the partial and semipartial R^2 were calculated for each. Partial R^2 is the amount variance of the response variable explained by a predictor variable from which the explained variance of the other predictors has been partialed or controlled (Cohen et al., 2003; Kim, 2015; Figure 1.2). Semipartial R^2 is the amount variance of a response variable that is uniquely explained by a predictor variable, and is independent of the other predictor variables (Cohen et al., 2003; Kim, 2015; Figure 1.2).

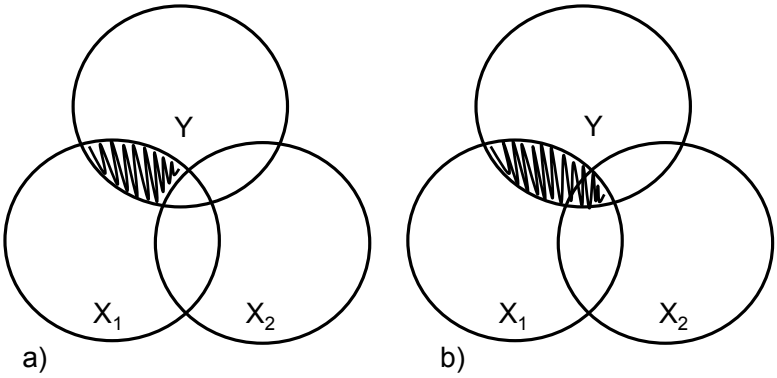

Figure 1.2. Simplified ballantine Venn diagrams of the explained variance of predictor variable X_1 on response variable Y. Overlap of the circles represents the amount of Y's variance explained by X_1 and X_2. The portion of Y that has no overlap with (i.e., cannot be explained by) X_1 and X_2 is the error: a) shows the spr^2, the amount of Y's variance uniquely explained by X_1; b) shows the pr^2, the amount of Y's variance explained by X_1 which controls for the amount of Y's variance explained by X_2.

Non-linear regression was used to test the effects of measured corn density within each site. An asymptotic model modified to pass through the origin was fit using the nls function (package MASS):

$$Y = asym(1 - e^{(-e^{lrc \times CD})})$$

where Y is the corn yield (g m^{-2}); $asym$ is the asymptote (i.e., the maximum grain yield when corn planting density approaches infinity); lrc is the natural logarithm of the rate constant (i.e., the corn density to reach half of the asym); and CD is the measured corn density (plants m^{-2}). Data used for non-linear regression analyses were from 'No Corn', 'Low', 'Medium', and 'High' treatments.

The effect of interseeded cover crops on weed biomass and corn grain yield was also analyzed using linear mixed effect models (packages lme4 and lmerTest) with block as a random effect. Site and treatment were used as fixed effects. Data were taken from 'Medium', and 'Medium Control' treatments. ANOVAs were used to

determine if fixed effects or interactions were significant. LSmeans (package lsmeans) was used to assess the difference in mean August and October weed biomass, and yield; significant differences of means ($P \leq 0.05$) were determined using Tukey's adjustment.

RESULTS AND DISCUSSION

Weather

Across all sites, the corn-growing season in 2016 was hotter and drier than the 30-year average (Tables 1.2 and 1.3).

Table 1.2. Cumulative growing degree days (GDD) in 2016 for experimental sites compared to the long-term average§ (LTA) from 30 years of data. GDDs are base 10°C and were calculated from site-specific weather stations for time periods of corn planting to harvest (CPH), cover crop interseeding to first cover crop sample date (CC 1) and cover crop interseeding to second cover crop sample date (CC 2).

GDD time period	New York	Pennsylvania	Maryland
CPH	1445	1466	1968
CPH LTA	1231	1196	1729
CC 1	593	526	783
CC 1 LTA	516	453	708
CC 2	1154	1082	1518
CC 2 LTA	941	888	1328

§ The 30-year GDD averages were calculated from *climatesmartfarming.org/tools/csf-growing-degree-day-calculator*.

Table 1.3. Average monthly precipitation (cm) in 2016 for experimental sites compared long-term average§ (LTA) from 30 years of data.

Month	New York	Pennsylvania	Maryland
May	1.6	1.6	13.1
May LTA	8.0	8.8	11.0
June	1.4	6.7	12.0
June LTA	9.5	10.4	9.4
July	4.4	4.1	14.9
July LTA	8.9	8.9	10.0
August	5.5	0.8	10.7
August LTA	8.0	9.8	8.3
September	5.3	1.2	7.6
September LTA	10.2	9.1	10.4
October	20.5	4.3	1.9
October LTA	8.7	7.7	9.3

§ Data for 2016 were complied from site-specific weather stations, 30-year averages were found at *https://www.ncdc.noaa.gov/cdo-web/datatools/normals*.

Effects of crop density treatments across sites

A corn density gradient was successfully established across the different planting rate treatments at each site, but a significant interaction between site and treatment was observed (Table 1.4). All Pennsylvania treatments had lower corn density than New York and Maryland. It is likely that drought conditions in Pennsylvania resulted in low emergence of corn from both the initial seeding and subsequent replanting (Sangoi, 2001). An interaction between site, sample date, and treatment was observed for light transmission (Table 1.4). This interaction can likely be explained by differences in corn densities and also corn growth rates across sites.

Table 1.4. The effect of site, treatment, and sample date on corn density, light transmission, log-transformed weed biomass (g m^{-2}), log-transformed cover crop biomass (g m^{-2}), and corn grain yield (g m^{-2}) using data from 'No Corn', 'Low', 'Medium', and 'High' treatments in all sites.

Fixed effects	Corn density	Light transmission	Weed biomass†	Cover crop biomass†	Corn yield
Site (S)	<0.001	0.05	<0.001	0.083	<0.001
Treatment (T)	<0.001	<0.001	<0.001	<0.001	<0.001
S × T	<0.001	<0.001	0.87	<0.001	<0.001
Sample date (SD)	–§	0.12	<0.001	<0.001	–
S × SD	–	<0.001	0.11	0.03	–
TX × SD	–	<0.001	0.006	0.25	–
S × SD × TX	–	0.02	0.50	0.81	–

§ Dash indicates effect or interaction inappropriate for response variable
† Dry weight biomass was ln(x + 1) transformed for analysis

We observed a site by treatment interaction and a site by sample date interaction for cover crop biomass (Table 1.4). Site differences in cover crop biomass could be due to different weather and soil conditions. Weed biomass varied by site and we observed an interaction between treatment and sample date. In treatments with corn, weed biomass tended to be greatest in Pennsylvania and lowest in New York. In 'No Corn' treatments, weed biomass in Maryland was greatest. Although increasing crop density can be a useful tool for suppressing weeds (e.g., Teasdale, 1998; Weiner et al., 2001), the 'Medium' and 'High' treatments had similar ranges of weed biomass in this experiment. An interaction was observed between site and treatment for corn grain yield, which is likely due to difference in corn densities across sites (Table 1.4).

Relationships between corn density and light transmission, weed biomass, and cover crop biomass within each site

The relationships between measured corn density and light transmission, weed biomass, and cover crop biomass were tested with linear regression within each site for each sample date. Overall, results support our hypothesis that light transmission, cover crop biomass, and weed biomass would decrease as corn planting density increased. However, in Pennsylvania we found no relationship between weed biomass, at either sample date, and corn planting density.

Light Transmission

We found a negative relationship ($P < 0.001$) between corn planting density and light transmission in all sites and at both sample dates (Table 1.5, Figure 1.3). The effect of corn density on light transmission strengthened from the first to the second sample date, which can be seen in the slope of the regression lines at the two sample dates. These results are consistent with previous research. Tollenaar et al. (1994), Westgate et al. (1997), Teasdale et al. (1998), and Andrade et al. (2002) all found a significant reduction in light transmission at ground level when corn planting density was increased. In high density corn most light is captured by young leaves at the top of the canopy, and in low density corn the light which is not captured by the top leaves can be captured by those lower on the plant (Loomis et al., 1968). Similar to our findings at the August sample date, Rajcan and Swanton (2001) reported that corn planted at recommended planting rates resulted in approximately 10% light

transmission below the top 1 m of the corn canopy at corn tasseling (Rajcan and Swanton, 2001). Tollengaar et al. (1994) found light transmission at corn silking ranged from 14.9% at 4 plants m^{-2} to 8.1% at 7 plants m^{-2} to 4.2% at 10 plants m^{-2}, but the trend in transmission was reduced and became more uniform across planting densities when weeds were present (Tollenaar et al., 1994).

Weed Biomass

Dominant weed species varied by site. In New York, the most frequently occurring species (occurance > 50%) in decreasing order were common lambsquarters (*Chenopodium album* L.), pigweeds (*Amaranthus spp.* L.) and common ragweed (*Ambrosia artemisiifolia* L.). In Pennsylvania, the most frequently occurring species (occurance > 50%) in decreasing order were giant foxtail (*Setaria faberi* Herm.), velvetleaf (*Abutilon theophrasti* Medik), common lambsquarters and pigweeds. In Maryland, the most frequently occurring species (occurance > 50%) in decreasing order were barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) and pigweeds.

A negative relationship was observed between corn planting density and weed biomass in New York and Maryland, but not in Pennsylvania (Figure 1.3). The regressions for New York and Maryland are congruent with previous research. Tollengaar et al. (1994) found that increasing corn plant density from 4 to 10 plants m^2 reduced weed biomass by up to 50%. However, Teasdale (1995), found increasing corn population density was a poor method for weed control, because the cost of seed for higher planting rates was not offset by gains in yield. The regressions for New

York and Maryland show that if corn is planted at higher seeding rates, there will be less weed biomass. This interpretation should be applied cautiously because the trend may be influenced by the weed biomass in 'No Corn' treatments. A more appropriate conclusion is that weed biomass in planted treatments was reduced only when compared to the 'No Corn' treatments in New York and Maryland.

The regression in Pennsylvania showed no relationship ($P > 0.05$) between corn planting density and weed biomass, so weed biomass was similar across treatments. It is likely that drought at this site slowed the development of the corn and so canopy closure was delayed (Çakir, 2004). Reduced competition from the corn may have allowed the weeds in Pennsylvania to be more competitive and evenly distributed throughout treatments. It is also possible that the lack of weed suppression was due to the lower corn density that was achieved at this site compared to the other sites.

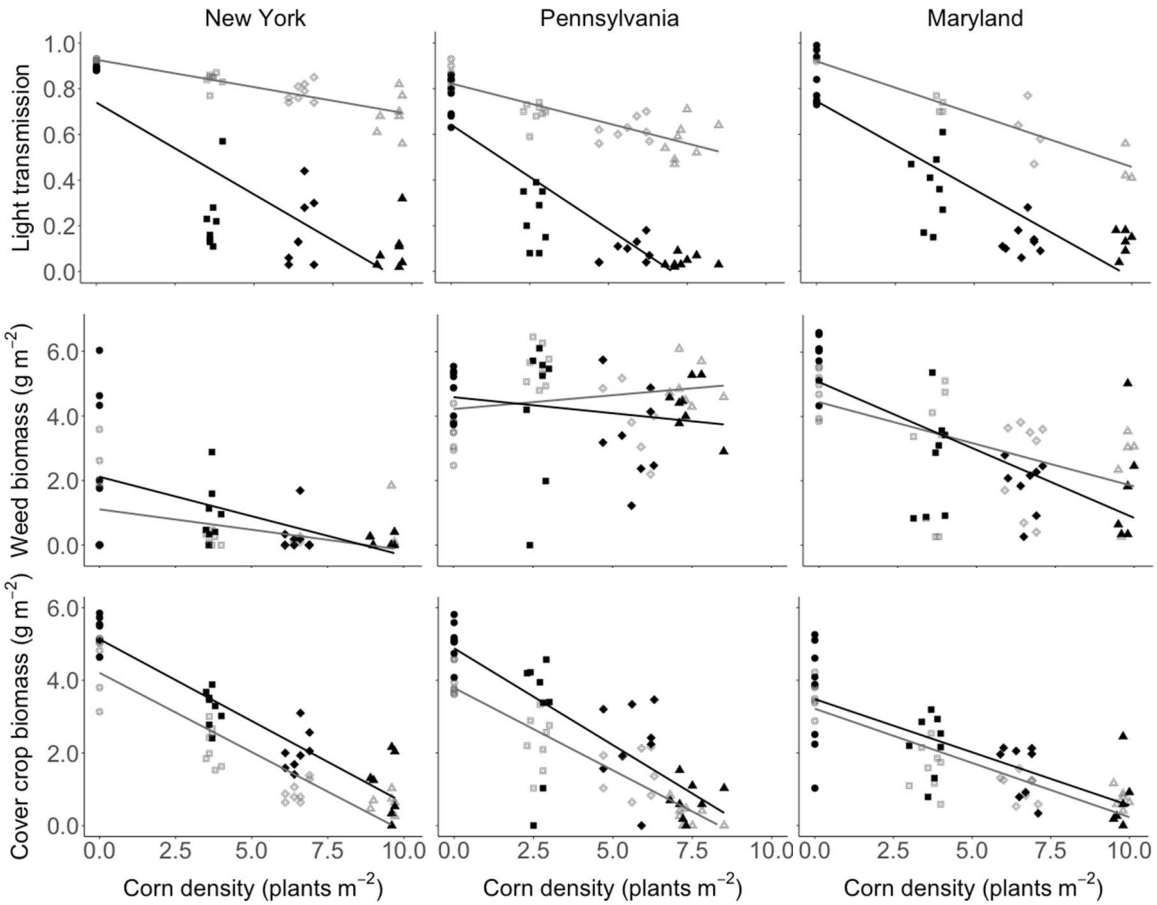

Figure 1.3. The effect of corn density on light transmission, interseeded cover crop biomass, and weed biomass in the three experimental sites. All dry weight biomass data were log-transformed [ln(x + 1)] to deal with zeros. The grey points and regression line are data from the June sample date for PAR data, and the August sample date for biomass data. The black points and regression line are data from August sample date for PAR data and the October sample date for biomass data. Circles are data from 'No Corn' treatments, squares are data from 'Low' treatments, diamonds are data from 'Medium' treatments, and triangles are data from 'High' treatments. Equations for each regression line and associated R^2 and p-values are in Table 1.5.

Table 1.5. Regression equations and associated R^2 and P-values for six response variables (RV) to corn planting density (CD). Response variables include June light transmission (JLT), August light transmission (ALT), log-transformed† August weed biomass (AWB; g m^{-2}), log-transformed† October weed biomass (AWB; g m^{-2}), log-transformed† August cover crop biomass (ACCB; g m^{-2}), and log-transformed† October cover crop biomass (ACCB; g m^{-2}).

	New York			Pennsylvania			Maryland		
RV ~ CD	Equation	R^2	P	Equation	R^2	P	Equation	R^2	P
JLT	- 0.02x + 0.93	0.74	<0.001	- 0.04x + 0.82	0.69	<0.001	- 0.04x + 0.91	0.79	<0.001
ALT	- 0.08x + 0.74	0.68	<0.001	- 0.09x + 0.64	0.77	<0.001	- 0.07x + 0.73	0.74	<0.001
AWB	- 0.12x + 1.10	0.2	0.006	0.09x + 4.22	0.02	0.21	- 0.24x + 4.39	0.25	0.002
OWB	- 0.24x + 2.10	0.29	<0.001	- 0.10x + 4.59	0.01	0.27	- 0.39x + 4.98	0.46	<0.001
ACCB	- 0.43x + 4.18	0.84	<0.001	- 0.45x + 3.79	0.83	<0.001	- 0.28x + 3.18	0.75	<0.001
OCCB	- 0.47x + 5.30	0.87	<0.001	- 0.53x + 4.88	0.66	<0.001	- 0.28x + 3.44	0.51	<0.001

† Dry weight biomass was ln(x + 1) transformed for analysis.

Cover crop biomass

A negative relationship between corn planting density and cover crop biomass was observed at all sites at both sampling dates (Table 1.5, Figure 1.3). Unlike the relationship between measured corn density and light transmission, the slope of the relationship with cover crop biomass was fairly consistent across the two sampling dates. Baribatsu et al., (2008) drill interseeded cover crops into a corn planting density gradient of 37, 500 to 70, 000 plants ha^{-1} and found a significant negative relationship with cover crop dry weight, with an average range over three years of 4.25 – 3.6 Mg ha^{-1}. Few, if any, other studies have examined drill interseeded cover crops in a corn planting density gradient. However, research with cover crops that were broadcast seeded into a cereal crop showed that cover crop biomass decreased with increased planting density of the cereal crop. For example, Ross et al. (2003) found biomass of interseeded Berseem clover (*Trifolium alexandrinum* L.) was reduced by 58–60%, 68–75 and 80–82% in oat densities of 25, 50, and 100 live seeds m^{-2}, respectively, compared to a no oat control.

Direct and indirect effects on cover crop biomass

Linear regression analyses showed a strong negative relationship between corn planting density and light transmission, corn planting density and weed biomass, and cover crop biomass. However, the relationships between light transmission and cover crop biomass, light transmission and weed biomass, and cover crop and weed biomass could not be correctly analyzed due to the confounding effect of corn planting density.

Path analysis was used to parse out which predictor, corn planting density, light transmission, or weed biomass had a greater effect on cover crop biomass. Moreover, path analysis was used to determine if the effect of corn planting density on cover crop biomass is mediated through light transmission and weed biomass. The following path model was used:

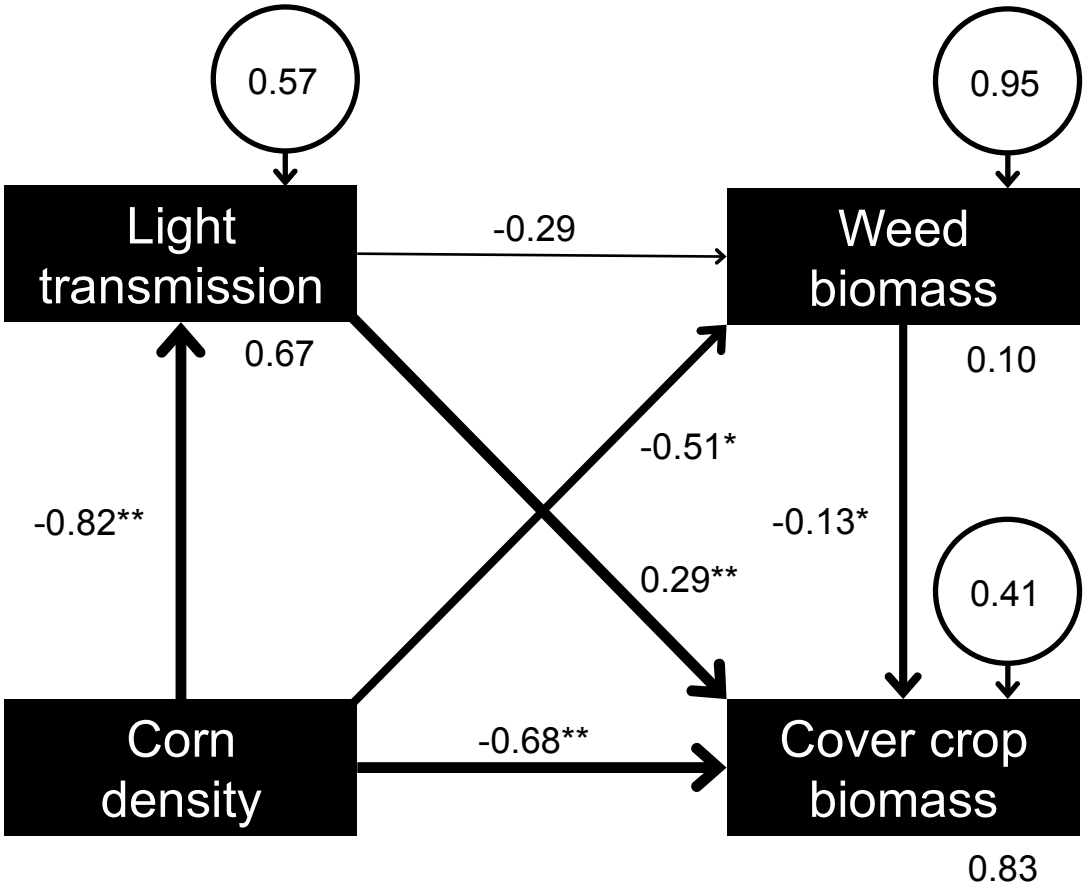

Figure 1.4. Path diagram of factors influencing interseeded cover crop biomass. Arrows indicate a direct effect of one variable on another. Numbers on the bottom right of a variable box is its R^2 value. Numbers in circles are the error terms associated with the variable to which the arrow points. Asterisks next to coefficients refer to significance level where * = $P < 0.01$, ** = $P < 0.001$.

In this path model, measured corn density, light transmission, and weed biomass each have a direct effect on cover crop biomass. Corn density has three indirect effects on cover crop biomass: one mediated by light transmission, one mediated by weed biomass, and one mediated by light transmission and weed biomass (Figure 1.4). The path coefficient corresponding to the arrow between corn density and light transmission represents a standardized simple regression relation. The path coefficients corresponding to the arrows between corn density and cover crop biomass, light transmission and cover crop biomass, and weed biomass and cover crop biomass represent partial coefficients. A partial coefficient is the expected change in the dependent variable associated with a unit change in a given predictor that controls for the covarying effect of another predictor (Grace and Bollen, 2005). The error terms associated with light transmission, weed biomass, and cover crop biomass are calculated as $\sqrt{1 - R^2}$. R^2 is calculated for each variable from the model (Ryan et al., 2011). Corn density, light transmission, and biomass are all in different units, so coefficients calculated from the raw data are difficult to interpret comparatively. To avoid this problem, coefficients were standardized (Grace and Bollen, 2005). Ten parameters were estimated for this model, six path coefficients and four variances; the model is therefore Just Identified (Parry, 2017).

Table 1.6. Direct and indirect path coefficients of the path diagram from figure 1.4. Variables were corn density (CD), August light transmission (LT), log-transformed August cover crop biomass (CCB; g/m^2), and log-transformed August weed biomass (WB; g/m^2). For direct effect path types, path coefficients are the effect of the variable to the left of the → (*x*) on the variable to the right of the → (*y*). For indirect effect path types, path coefficients are effect of the leftmost variable on the rightmost variable, as mediated by the variable(s) between →'s. P is the p-value for path coefficient. The estimate for the path coefficient can be interpreted as the expected change in standard deviation units of *y* with an increase of 1 standard deviation unit of *x*.

Path type	Path	Coefficient	P
Direct	CD → LT	-0.82	<0.001
	CD → WB	-0.51	0.003
	CD → CCB	-0.68	<0.001
	LT → WB	-0.29	0.08
	LT → CCB	0.29	<0.001
	WB → CCB	-0.13	0.004
Indirect	CD → LT → CCB	-0.24	<0.001
	CD → LT → WB	0.24	0.09
	CD → WB → CCB	0.07	0.04
	LT → WB → CCB	0.04	0.14
	CD → LT → WB → CCB	-0.03	0.14
Error	LT	0.57	<0.001
	WB	0.95	<0.001
	CCB	0.41	<0.001

An indirect effect is calculated as the product of component direct effects. For example, the direct effect of corn density on light transmission is -0.82, and the direct effect of light transmission on cover crop biomass is 0.29, so the indirect effect of corn density on cover crop biomass as mediated by light transmission is -0.24. The total effect of corn density on cover crop biomass can be calculated from the sum of all the direct and indirect path coefficients of corn density on cover crop biomass (-0.88). An example of model interpretation is as follows: a one standard unit increase in corn

density would directly change cover crop biomass by -0.68 standard deviation units, and indirectly (mediated through light transmission) by -0.24 standard deviation units.

The results from the path analysis support our hypothesis that the effect of corn planting density on cover crop biomass would be mediated by light transmission and weed biomass. Specifically, the path analysis showed that corn density, light transmission, and weed biomass had significant direct effects on cover crop biomass, but corn density had the greatest effect. The indirect effect of corn density on cover crop biomass was significant, as mediated by either light transmission or weed biomass, but not when mediated by light transmission and weed biomass. It was also determined that light transmission did not have a significant direct effect on weed biomass (Table 1.7).

Partial and semipartial correlation

To assess the proportion of variance in cover crop biomass that was explained by corn density, light transmission, and weed biomass, we used multiple linear regression and compared the partial R^2 (pr^2) and semipartial R^2 (sr^2) for each predictor variable (Table 1.7). Corn density explained 44% of the variance in cover crop biomass when the effect other two variables was controlled. Light transmittance explained 13% of the variance in cover crop biomass when the effect other two variables was controlled. Weed biomass explained 8% of the variance in cover crop biomass when the effect other two variables was controlled. Corn density, light

transmission, and weed biomass uniquely accounted for 13%, 4%, and 7% of variance in cover crop biomass, respectively.

The results from path analysis and partial and semipartial correlation reinforce the same trends. For example, path analysis showed that corn density had the greatest effect on cover crop biomass, while partial and semipartial correlation showed that corn density accounted for the most variance in cover crop biomass. These analyses are independent but complementary ways of understanding the interrelations of a network of variables: path analysis quantifies the effects of predictor variables, and partial and semipartial correlation quantify the explained variance by each predictor variable.

Table 1.7. The proportion of variance in cover crop biomass as explained by bivariate (R^2), partial (pr^2) and semipartial (sr^2) coefficients of determination for the predictor variables corn density, light transmission, and weed biomass. Multicollinearity was assessed with variance inflation factors (VIF), where a value > 10 indicates severe multicollinearity.

Predictor	VIF	R^2	pr^2	sr^2
Corn density	3.4	0.78	0.44	0.13
Light transmission	3.2	0.69	0.13	0.04
Weed biomass	1.1	0.01	0.08	0.07

Effect of corn density on corn grain yield within each site

The relationship between corn grain yield and measured corn density as well as the maximum grain yield was assessed for each site separately using non-linear regression. In New York, the maximum predicted corn grain yield was 1132 g m^{-2} (Table 1.8). Corn grain yield in New York was relatively high, especially considering the drought conditions early in the season. In Pennsylvania, the maximum predicted

corn grain yield was 928 g m^{-2} (Table 1.8). Corn density in Pennsylvania did not exceed 8 plants m^{-2}, so it is possible that asymptotic yield could have been achieved had the corn population densities better reflected the intended planting rates. In Maryland, the maximum predicted corn grain yield was 750 g m^{-2} (Table 1.8). Corn grain yield in Maryland was relatively low, especially considering the longer potential growing season compared to New York. Teasdale et al., (2012) planted corn in the same field from 2008 - 2010; their corn was planted at 80,300 plants ha^{-1} at dates and weed biomass similar to ours and their yield ranged from 3.00 - 9.25 Mg ha^{-1} in weedy plots. The mean Maryland yield for this experiment was within the range from (~7.43 Mg ha^{-1}) and so should be considered normal for this site.

Table 1.8. Result summary of yield as a function of corn density nls models. Predicted estimates (Est), standard errors (SE), and p-values (P) for the parameters asymptotic yield (asym) and natural logarithm rate constant (lrc) are provided for each site. R^2 were calculated from the predicted Pearson residuals of each model.

Site	R^2	Parameter	Est	SE	P
NY	0.84	asym	1132	38.8	<0.001
		lrc	-0.7	0.17	<0.001
PA	0.9	asym	928	59.5	<0.001
		lrc	-1.2	0.16	<0.001
MD	0.75	asym	754	28.2	<0.001
		lrc	-0.3	0.34	0.4

Corn grain yield is negatively affected by reduced soil moisture and drought conditions (Sangoi, 2001, Rajcan and Swanton, 2001, Earl and Davis, 2003), weed competition (Cousens, 1985), and soil structure (Triplett et al., 1970), which may all help explain differences in yield across sites. Yield is also dependent on the plasticity of the corn hybrid (Thompson and Jordan, 1995, Sarlangue et al., 2007).

Despite drought conditions and weed pressure, average New York yield exceeded average 2016 Cayuga County yields (1051g m^{-2} compared to 784.6 – 940.9 g m^{-2}), and average Pennsylvania yield exceeded average 2016 Huntington's County yields (703 g m^{-2} compared to 627.7 g m^{-2}). Average Maryland yield was slightly less than average 2016 yield for the counties surrounding Prince George County (734.8 g m^{-2} compared to 784.6 g m^{-2}) (USDA, 2016; Table Y).

The small difference between yield in 'Medium' and 'High' treatments in Pennsylvania, and all planting treatments in New York and Maryland, was probably because of the flex-ear corn hybrid (Thomison and Jordan, 1995), which was planted at near-optimal rates. Cox (1997) planted flex ear hybrids with similar relative maturities in a density gradient ranging from approximately 30,000 to 89,000 plants ha^{-1}: In a dry year, he determined the optimal density to be approximately 86,000 plants ha^{-1} (Cox, 1997). Flex-ear traits allow the corn plant to respond to planting density, whereby it can grow a second ear if it senses low crowding by its neighbors (Nielson, 2005). 'Low' treatments in New York and Maryland probably were able to add another ear. 'Low' treatments in Pennsylvania had much lower yield than other treatments probably because weed pressure (Cousens, 1985); drought should not have inhibited a positive flex response in the Pennsylvania 'Low' treatment (Cox, 1997; Miller et al., 1995).

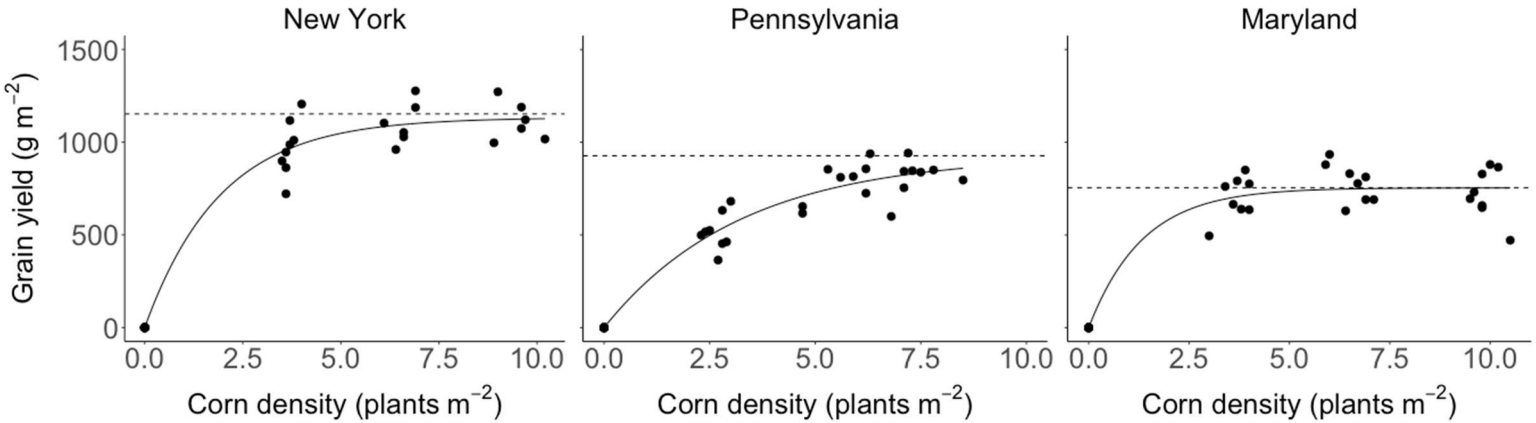

Figure 1.5. The effect of corn density on grain yield at each site. The dashed line corresponds to the predicted asymptote from the model, which can be interpreted as the maximum predicted yield.

Effects of interseeded cover crops on weed biomass and corn grain yield

The mean August and October weed biomass, and yield were compared between the 'Medium' and 'Medium Control' treatments to determine if interseeded cover crops had a weed suppression effect or negative impact on corn yield. It was expected that the 'Medium' treatment would have less weed biomass than 'Medium Control' because cover crop biomass in general (e.g., Pullaro et al., 2006) and interseeded cover crop biomass specifically (Uchino et al., 2015) have been shown to suppress weeds. Uchino et al. (2015) found interseeded cover crops to suppress inter-row weeds in maize throughout the growing season. Brainard et al., (2004) found weed suppression by interseeded cover crops was minimal in transplanted cabbage, however. It was expected that there would be no yield difference between the treatments because cover crops were interseeded after the V5 stage of corn when there is no competition between corn and the cover crop (Curran et al. *In Press*).

The results from the ANOVA (Table 1.9) determined a significant interaction in mean August weed biomass between site and treatment, a significant difference in mean October weed biomass in both site and treatment, and a significant difference in mean yield between sites, (Table 1.9).

The results show that there was no suppressive effect by interseeded cover crops on August weed biomass, but there was a suppressive effect in October, where weed biomass was less in 'Medium' than 'Medium Control' treatments averaged across sites. Uchino et al. (2012 and 2015) found interseeded cover crops to suppress weeds as early as 150 GDD (°C) after interseeding (approximately 40 days after

interseeding) in a cool summer growing season where maximum temperatures ranged from 16.6 – 23.8°F. Cover crops perform better in systems where they do not need to compete for water and nutrients (Snapp et al., 2005), so it is possible that the weed suppression ability of cover crop in this experiment was inhibited because of drought conditions. We found support our hypothesis that weed biomass would be suppressed from interseeded cover crops at the October sampling date only.

Table 1.9. Results of ANOVA and LSmeans to determine the effect of presence/absence of interseeded cover crops on August and October weed biomass and corn yield. Site refers to the three experimental sites New York (NY), Pennsylvania (PA), and Maryland (MD). Treatment refers to the 'Medium' (CC) and 'Medium Control' (NCC) treatments, which were planted at 74,100 plants ha^{-1} with corn, with and without interseeded cover crops, respectively. P-values refer to the F-test in the ANOVA. Similar letters next to means within a column indicate no significant difference ($\alpha = 0.05$). Dry weights of weed biomass were log-transformed for analyses and back-transformed for presentation.

Effect	August weed biomass		October weed biomass	Corn grain yield
	----------p-value----------			
Site (S)	<0.001		<0.001	0.02
Treatment (T)	0.4		0.01	0.56
S × T	0.04		0.24	0.96
LSmeans	----------(g m^{-2})----------			
NY	–§		1.88 B	1026 A
PA	–		62.18 A	745 B
MD	–		7.24 B	830 B
NCC	–		13.87 a	–
CC	–		6.42 b	–
NY × NCC	1.40	n.s.	–	–
NY × CC	1.06		–	–
PA × NCC	89.12	n.s.	–	–
PA × CC	67.36		–	–
MD × NCC	3.60	*	–	–
MD × CC	13.20		–	–

§ Dash indicates effect or interaction should not be interpreted

n.s. Indicates no significant difference * Indicates a significant difference at $\alpha = 0.05$

Summary and Management Implications

We set out to determine how cash crop management practices affect interseeded cover crop performance during the transition to certified organic production. We observed a tradeoff between corn density and cover crop biomass. Path analysis showed that the effect of corn planting density on interseeded cover crop biomass was significant when quantified both directly and indirectly as mediated by light transmission and log-transformed weed biomass. Partial and semi-partial correlation quantified the controlled and unique variances explained by corn density, light transmission and weed biomass on cover crop biomass. Path analysis and partial and semi-partial correlation are complementary analyses that can be used to determine if trends in the magnitude of effect and explained variance are consistent across predictors. Weed biomass in treatments with- and without drill interseeded cover crops was significantly lower in plots with cover crops at the October sample date. No difference in corn grain yield was observed between treatments with and without cover crops. Results from this experiment should be interpreted cautiously because the experiment used one corn hybrid and was conducted during a dry year.

Overall our results suggest that farmers can increase the performance of interseeded cover crop by using flex ear varieties and corn planting rates that are slightly lower what is typically used without reducing corn grain yield. It is likely that acceptable corn yields can be achieved from this flex ear corn planted at approximately 75,000 plants ha^{-1}. The cover crop biomass in this planting density

ranged approximately 1.6 to 54.0 g m^{-2} dry weight, back transformed from analyses, across all sites and sample dates. Additional research should be conducted to determine the corn planting density that maximizes corn yield and cover crop biomass across a wider range of environments.

Given that organic farmers routinely use cover crops and that the cost of cover crop seed is inherent to organic production, future research should also determine how costs and benefits (e.g. improved soil health, reduced fertilizer requirements, lower weed seed production, etc.) related to interseeding a grass-legume cover crop mixture compared to standard post harvest cover crop seeding.

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CHAPTER 2

COVER CROP AND WEED SEED PREFERENCE OF FOUR COMMON WEED SEED PREDATORS

ABSTRACT

Invertebrate seed predators (ISPs) are an important component of agroecosystems that help regulate weed populations. Previous research has shown that ISPs seed preference depends on the plant and ISP species. Although numerous studies have quantified weed seed losses from ISPs, limited research has been conducted on the potential for ISPs to consume cover crop seeds. Cover crops are commonly broadcast seeded, and because seeds are left on the soil surface they are susceptible to ISPs. We hypothesized that 1) ISPs will consume cover crop seeds as much as weed seeds, 2) seed preference will vary by plant and ISP species, and 3) seed consumption will be driven by seed morphology and nutritional characteristics. We conducted seed preference trials with four common ISPs (Pennsylvania dingy ground beetle, Common black ground beetle, Allard's ground cricket, Fall field cricket) in laboratory No Choice and Choice feeding assays to compare seed predation of ten cover crop species

(barely, annual ryegrass, pearl millet, forage radish, cereal rye, white mustard, crimson clover, red clover, triticale, hairy vetch) and three weed species (velvetleaf, common ragweed, giant foxtail). We found all four ISPs readily consume cover crop seeds and that cover crops with hard seed coats and seed hulls such as hairy vetch and barley are generally not preferred. In No Choice trials, the maximum proportion of seeds consumed was 0.75, 0.50, 0.47, and 1.0 for the Pennsylvania dingy ground beetle, the common black ground beetle, Allard's ground cricket, and the fall field cricket, respectively. Our results suggests that farmers should select cover crop species that are avoided by ISPs if they plan on broadcasting the seed, such as with aerial interseeding.

INTRODUCTION

Invertebrate seed predators (ISPs) such as carabid beetles (Coleoptera: Carabidae) and crickets (Orthoptera: Gryllidae) are key drivers of weed seed destruction (Westerman et al. 2003; Kulkarni et al. 2015a) and the subsequent reduction of weed emergence (White et al. 2007; Kulkarni et al. 2015b). ISPs can consume seeds before seed dispersal (pre-dispersal predation) or once the seeds have been shed and are on the soil surface (post-dispersal). Pre-dispersal predation tends to be very species specific and does not usually cause large weed seed losses (Nurse et al. 2003), whereas post-dispersal predation is usually carried out by multiple generalist seed predators and can have large impacts on weed population dynamics (Crawley 1992). Field studies have shown that landscape context and farm-management factors influence ISP activity-density and weed seed predation rates (e.g., Trichard et al. 2013; Petit et al. 2017). However, these field studies are limited in the number of weed species they can evaluate at one time. Preference trials can be used to understand the effects of ISPs on weed community dynamics because the seed predation rates of

many weed species by multiple ISPs can be evaluated efficiently (e.g., Honek et al. 2007).

Laboratory feeding assays have been used to determine weed seed preference by ISPs and results determined in the lab often translate directly to field preference (e.g., Honek et al. 2006; Ward et al. 2014; Petit et al. 2014). In general, constraints such as ISP body size and mouthpart strength determine which seeds can be consumed (Honek et al. 2007; Lundgren 2009). Several species of carabid beetles such as *Amara aenea* (DeGeer; Ward et al. 2011), *Anisodactylus sanctaecrucis* (F.; White et al. 2007), *Harpalus affinis* (Schrankl; Honek et al. 2006), and crickets such as *Gryllus pennsylvanicus* (Burmeister; Carmona et al. 1999) and *Teleogryllus emma* (Ohmachi and Matsuura; Ichihara et al. 2012) have been evaluated for seed preference. However, the Pennsylvania dingy ground beetle (*Harpalus pensylvanicus* DeGeer) has been the model ISP species for preference work. Lundgren and Rosentrater (2007) found *H. pensylvanicus* preferred small, dense seeds with hard seed coats (e.g., Pigweed [*Amaranthus retroflexus* L.]; mass ~0.33 mg; seed coat strength ~47.81 MPa) compared to large seeds (e.g., Morning glory [*Ipomoea hederacea* L.]; mass ~24.65 mg; seed coat strength ~3.95 MPa). Ward et al. (2014) found *H. pensylvanicus* consumed 71% of presented giant foxtail seeds compared to < 1% of velvetleaf (*Abutilon theophrasti* Medik) seeds. Though the material properties of seeds play a large role in determining seed preference, nutrient regulation has been proposed as another driving factor of insect food selectivity (Behmer 2009).

When multiple food sources are available, insects select those that optimize ratios of macronutrients such as lipids, carbohydrates and proteins. These nutrient ratios determine the health, development and evolutionary fitness of individual insects (Simpson et al. 2015). The geometric framework is a state-space modeling approach that can be used to demonstrate how an insect maintains its required nutrient ratio by switching between nutritionally suboptimal but complementary foods (Behmer 2009). By applying the geometric framework for nutrition, Jensen et al. (2012) determined that the predatory carabid *Anchomenus dorsalis* (Pontoppidan) selected food to optimize a lipid to protein ratio of 0.36, which maximized the number of eggs a female could lay. Likewise, Harrison et al. (2014) found that spring field crickets (*Gryllus veletis* Alexander and Bigelow) consume food sources that give a protein to carbohydrate ratio of 1 to 4.1 for males and 1 to 2.3 for females

Laboratory seed preference of ISPs is generally studied in No Choice and Choice trials, but quantified in many different ways. In No Choice trials, seed from a single plant species is offered to a captive insect, whereas seed from multiple plant species are offered in Choice trials. In No Choice trials, Lundgren and Rosentrater (2007) presented 0.25 g of seed for each plant species, whereas Ward et al. (2014) presented 9 seeds regardless of seed size. In their Choice trials, Honek et al. (2007) presented 15 seeds of large seeded species (e.g., great burdock [*Arctium lappa* L.]) and 30 seeds of small seeded species (e.g., common lambsquarters [*Chenopodium album* L.]), while Ward et al. (2014) standardized by seed number in their Choice trials and offered 3 seeds each of velvetleaf, giant foxtail, and common lambsquarters.

Quantifying consumed seeds is also variable among researchers. Some authors consider a seed consumed when >50% has been destroyed (e.g., Honek et al. 2007), and others consider a seed consumed if the seed coat is cracked and some endosperm damaged (e.g., Carmona et al. 1999). Although methods vary in the literature, most ISP research has focused on assessing the ecosystem service of weed seed destruction and characterizing ISP ecology (Kulkarni et al. 2015a).

A great deal of literature (e.g., Kabaluk and Ericsson 2007; Reisig et al. 2017) exists on early season insect pests that feed on cash crop seeds, such as wireworms (*Agriotes* spp.), earworms (*Helicoverpa zea* Boddie) and seedcorn maggot (*Delia platura* Meigen), but there has been relatively little research on the effects of weed seed predators such as carabid beetles and crickets on crop seeds. One group of crops for which seed predation data might be particularly relevant is cover crops. Cover crops are an agroecological tool increasingly used in the US (Singer 2008; Wayman et al. 2016; SARE 2016), for the suite of ecosystem services they provide (Schipanski et al. 2014). Cover crops are normally seeded after cash crops are harvested in the fall, but there is increasing interest in establishing cover crops prior to cash crop harvest (e.g., Brainard et al. 2004; Baributsa et al. 2008; Uchino et al. 2015; Belfry and Van Eerd 2016; Blanco-Canqui et al. 2017). Compared to corn and soybean, which are typically planted or drilled into a furrow and then covered with soil, cover crops are often sown by broadcasting with a fertilizer spreader or aerial seeding with planes (Fisher et al. 2011; SARE 2016). Seeds on the soil surface are much more likely to be consumed by ISPs (White et al. 2007, Kulkarni et al. 2015b). For example, White et

al. (2007) found *H. pensylvanicus* consumed more giant foxtail (*Setaria faberi* Herm.) seeds on the soil surface compared to seeds buried at 0.5 cm. Wilson et al. (2014) reported losses of 48-98% of aerially seeded cover crop seeds one week after seeding them in southeastern Minnesota and hypothesized that seed predators were responsible for these losses.

Given that ISP seed preference is likely based on seed size and seed coat strength, cover crops that are similar to preferred weed seeds could also be consumed. The goal of this study was to assess the seed preference for common cover crop species by ISPs, and to compare their relative preference to common weeds that are known targets of ISPs. To quantify ISP preferences, a series of No Choice and Choice laboratory seed preference trials were conducted. We hypothesized that 1) ISPs will consume cover crop seeds as much as weed seeds, 2) seed preference will vary by plant and ISP species, and 3) seed consumption will be driven by seed morphology and nutritional characteristics.

MATERIALS AND METHODS

Laboratory Experiments

Ten cover crop species and three weed species were used to test seed preference of four weed seed predators (Table 2.1). These plant species were selected as they provide a spectrum of seed traits including weight, size, compressive yield strength, and oil and protein content. Weed seeds were collected from the Musgrave Research Farm in Aurora, NY in the fall of 2015 and kept in cold storage for the

winter. Germination of cover crop and weed seeds was tested prior the preference trial to verify their viability, and all plant species had at least 60% germination. Dry seeds were used in all trials. Within-species seed sizes were kept as similar as possible because size can influence seed viability in some species (e.g., Stanton 1984), which may affect ISP preference (e.g., Ward et al. 2014).

Four species of ISPs, including two carabid beetles and two crickets, were selected for preference trials (Table 2.2). These four species are common throughout agricultural fields the Northeast United States, and are relatively easy to catch. All beetles were collected with dry pitfall traps from Caldwell field at Cornell University in Ithaca, NY (42.45°N, 76.46°W) during the summer of 2016. Pitfall traps were made of 9 cm diameter nested plastic cups placed in the ground with the top flush with the soil. Pitfall traps were checked and reset each day. Pitfall traps were ineffective at catching crickets, so other capture methods were used to supplement cricket numbers. A butterfly net was used to capture *A. allardi* whereas *G. pennsylvanicus* were captured by hand. Specimens were brought back to the lab and their identification was verified using Bousquet (2010), Lindroth (1961), and Vickery and Kevan (1986).

Specimens were sorted into 10 x 15 cm clear plastic deli containers with a moist paper towel and small holes in the top of each container lid to permit air exchange. No more than 10 insects of the same species were placed in a single container. Containers were placed in a large plastic tub with a lid to maintain darkness, and the tub was stored in a refrigerator at 5-7°C for 4 days. Cool and dark conditions prevent cannibalism during the starvation period (Honek et al. 2003). The duration of

starvation used in this research was within the range reported in the literature as Honek et al. (2006) and Petit et al. (2014) starved for 5 days, Lundgren and Rosentrater (2007) and Ward et al. (2014) starved for 2 days, and White et al. (2007) starved for 1 day. After starvation, beetles and crickets were used in preference trials.

No Choice preference trials were used to determine the proportion of seeds consumed when seed from a single species was offered to the insect. No Choice trials occurred in 15 cm diameter petri dishes. A section of a 35 x 20 cm dry paper towel was inlayed into the wider half of the petri dish, and then 26 undamaged seeds, a wetted cotton ball atop a 2.5 cm^2 piece of plastic, and a single insect were then placed onto the paper towel. The narrower half of the petri dish was quickly replaced. The excess paper towel was folded over the outside of the narrower half of the petri dish to reduce light exposure and disturbance to the insect. All No Choice petri dishes were kept in the laboratory at ambient temperatures and daylight (Table 2.2). Petri dishes were kept out of direct sunlight.

Beetles and crickets were also used in Choice trials where all seeds of each plant species were offered to the insect at the same time. Choice preference trials were prepared using the same methods as the No Choice trials above, except that 2 seeds of each species were placed in each petri dish (total 26 seeds per dish). The number of replicate trials varied by ISP and plant species due to constraints related to insect capturing (Table 2.3).

Table 2.1. Seed descriptions for species included in preference trials. Seed weight was determined as average weight of 100 seeds divided by 100 to get mg per seed. Seed length and width were determined by the average measurements of 50 seeds. Seed volume was estimated as the volume of a cylinder (π*length*(0.5*width)^2). Strength is the compressive yield strength (i.e., the amount of force per unit area required to break the seed), and was estimated from the literature (references below); strength for references1-3 were reported in Newtons and converted to MPa based on our area measurements for each seed. Oil and protein are expressed as the % total seed weight. O:P is the oil to protein ratio of each seed species.

Scientific name	Common name	Mass (mg)	Length (mm)	Width (mm)	Volume (mm^3)	Strength (MPa)	Oil (%)	Protein (%)	O:P
Hordeum vulgare L.†	Barley	24.0	9.71	3.00	68.64	6.90[1]	1.30[6]	13.00[10]	0.10
Lolium multiflorum Lam. †	Annual ryegrass	3.1	5.28	1.40	8.13	--§	1.67[7]	9.50[7]	0.18
Pennisetum glaucum L. †	Pearl millet	5.8	3.24	1.89	9.09	--	5.78[7]	15.20[7]	0.38
Raphanus sativus L. †	Forage radish	16.7	3.88	2.96	26.70	--	40.85[7]	30.60[7]	1.33
Secale cereale L. †	Cereal rye	33.6	7.35	2.83	46.23	5.12[2]	4.90[7]	17.10[7]	0.29
Sinapis alba L. †	White mustard	4.7	2.19	2.00	6.88	--	31.50[7]	31.70[7]	0.99
Trifolium incarnatum L. †	Crimson clover	5.0	2.58	1.92	7.47	--	4.30[7]	40.95[7]	0.11
Trifolium pratense L. †	Red clover	1.5	1.96	1.45	3.24	--	8.55[7]	37.15[7]	0.23
× *Triticosecale* Witt. †	Triticale	41.0	7.64	3.25	63.38	8.74[3]	2.40[8]	12.50[11]	0.19
Vicia villosa Roth. †	Hairy vetch	22.7	3.52	3.29	29.92	11.92[4]	0.70[7]	30.20[7]	0.02
Abutilon theophrasti Medik.*	Velvetleaf	9.8	3.32	2.97	23.00	8.37 [5]	18.70[7]	12.90[7]	1.45
Ambrosia artemisiifolia L.*	Common ragweed	4.8	3.84	2.12	13.55	0.59 [5]	18.31[9]	22.62[9]	0.83
Setaria faberi Herm.*	Giant foxtail	1.2	2.36	1.34	3.33	8.74 [5]	6.73[7]	16.43[7]	0.41

[1]Bargale and Irudayaraj 1995; [2]Dziki and Laskowski 2007; [3]Babic et al. 2010 (taken as the average for three wheat varieties); [4]Rybiński et al. 2009 (from the related *V. sativa*); [5]Lundgren and Rosentrater 2007; [6]Ryan et al. 2007; [7]Royal Botanic Gardens Kew 2017; [8]Price and Parsons 1975; [9]Roedel and Thornton 1942; [10]Stoger et al. 2005; [11]Linnemann and Dijkstra 2002.

† Cover crop species; *weed species; § a dash indicates no data are available.

Table 2.2. Descriptions of insects used for preference trials and temperature and light data for trial dates. Ave day is average length of visible light for the date range. Temp day and Temp night are the average day and night temperatures (°C) for the date range. Data from www.wunderground.com.

Species type	Scientific name	Common name	Trial	Date range	Ave day	Temp day	Temp night
Carabid beetle	*Harpalus pensylvanicus* (DeGeer)	Pennsylvania dingy ground beetle	No Choice	Aug 21 – Jul 27	14h 30min	25.5	13.9
			Choice	Aug 7 – Aug 13	15h 15min	31.1	17.2
	Pterostichus melanarius (Illiger)	Common black ground beetle	No Choice	Jun 24 – Jul 8	16h 23min	28.3	14.4
			Choice	Jul 18 – Jul 22	16h 00min	30.0	15.0
Cricket	*Allonemobius allardi* (Alexander and Thomas)	Allard's ground cricket	No Choice	Aug 7 – Sep 27	14h 30min	25.5	13.9
			Choice	Sep 25 – Sep 30	13h 00min	18.3	13.9
	Gryllus pennsylvanicus (Burmeister)	Fall field cricket	No Choice	Aug 7 – Sep 9	15h 00min	26.7	13.9
			Choice	Sep 25 – Sep 30	13h 00min	18.3	13.9

Table 2.3. The number of Choice and No Choice replicate trials of each plant species for all ISPs.

Trial	*Harpalus pensylvanicus*	*Pterostichus melanarius*	*Allonemobius allardi*	*Gryllus pennsylvanicus*
		----------Number of replicate trials----------		
No Choice	20	19 common ragweed 20 all others	10 crimson clover 11 all others	7 cereal rye, wild radish, velvetleaf, barley 6 all others
Choice	20	20	20	11

Statistical Analyses

All analyses were done with R version 3.2.2 (R Core Team 2015). Data from No Choice and Choice trials were analyzed separately. Plant species (cover crop and weeds) were compared within each of the four ISPs. In a separate analysis, preference for individual plant species was compared across the four ISPs.

No Choice Trials

No Choice ISP seed preference was assessed with generalized linear mixed models. Seed predation was formed into a vector, using the *cbind* function of the number of seeds damaged and total seeds given, and analyzed using the binomial distribution with a logit link. Models were initially assessed with the glmer function (package lme4). However, models were overdispersed (package blmeco) and required optimizers to extend the maximum number of model iterations for convergence. Therefore, following the decision tree in Bolker et al. (2009), models were reanalyzed with glmmPQL (package MASS). This function uses penalized quasi-likelihood to estimate the parameters of a model to maximize the probability of the observed data (Bolker et al. 2009). A mixed model ANOVA was first used to determine differences ($P \leq 0.05$) in the mean probability of seed consumption between weed seeds and cover crops seeds. For this planned contrast, seed type (cover crop or weed) was the fixed effect and plant species nested in container ID nested in collection date was used as a random effect.

The arithmetic mean of the proportion of seeds destroyed for each plant species was presented in bar charts. Two separate models were used to determine

significant differences ($P \leq 0.05$) in the mean probability of seed consumption. One model tested for differences across plant species within each of the four ISPs. Another model tested for differences across ISPs within each of the thirteen plant species. Least square means (package lsmeans) was used to test for differences in both models. Statistically similar means were grouped using the cld function (package lsmeans) with Bonferroni correction. Groups with larger means were interpreted to have a greater probability of being consumed. In cases where the mean probability of seed consumption was either 0 or 1 and had a variance of 0, the seed was removed from analysis and assigned a letter of highest or lowest rank, independent of the cld groupings. All tests were on the logit scale.

Choice Trials

Choice ISP seed preference was first assessed with Vanderploeg and Scavia's electivity index E* (Vanderploeg and Scavia 1979). This index provides an intuitive measure for assessing food preference and has been applied to many different animal systems (e.g., Averill et al. 2016; Dupuy et al. 2016).

E* is calculated as:

$$E_i^* = \frac{W_i - \frac{1}{n}}{W_i + \frac{1}{n}}$$

Where W_i is:

$$W_i = \frac{(r_i/p_i)}{\sum (r_i/p_i)}$$

W_i is the selectivity coefficient, n is the number of food species in the trial, r_i is proportion of food species i consumed of all species consumed, and p_i is the proportion of food species i in the total food species offered. E* varies between -1 and 1. A positive E* indicates preference and a negative E* indicates avoidance; 0 E* indicates random preference.

A mixed effect ANOVA was first used to determine differences ($P \leq 0.05$) in the mean E* between weed seeds and cover crops seeds, using a similar planned contrast approach as with the No Choice trials. Linear mixed effect models were used to test the effect of seeds species on E*, with container ID nested in date of insect capture used as a random effect. Two separate models were used to determine significant differences ($P \leq 0.05$) in the mean E*. One model tested for differences across plant species within each of the four ISPs. Another model tested for differences across ISPs within each of the thirteen plant species. Least square means (package lsmeans) was used to test for differences in both models. Statistically similar means were grouped using the cld function (package lsmeans) with Bonferroni correction. In cases where the mean E* was 0 and had a variance of 0, the seed was removed from analysis and assigned a letter of lowest rank, independent of the cld groupings.

Seed traits

Relationships between seed consumption and seed morphological and nutritional traits were tested separately for each ISP using linear regression. The seed

traits were 1) mass (mg), 2) volume (mm^3), 3) compressive yield strength (MPa), 4) oil content (converted from % of seed weight to proportion of seed weight for analysis), 5) protein content (converted from % of seed weight to proportion of seed weight for analysis), and 6) the ratio of oil content to protein content (Table 2.1).

The effect of each trait was analyzed individually for a total of 12 seed trait regression models for each ISP (6 traits x 2 types of trials). No Choice ISP seed preference was assessed with generalized linear mixed models. Seed predation was formed into a vector, using the *cbind* function of the number of seeds damaged and total seeds given, and analyzed using the binomial distribution and logit link with the glmmPQL function. Seed trait was the fixed effect and seed species nested in container ID nested in collection date were random effects for each model. Choice ISP preference (using E* as proxy) was assessed with linear mixed effect models. Seed trait was the fixed effect and seed species nested in container ID nested in collection date were random effects for each model. The intercepts and slopes for each model are presented in Table 2.4. Choice trial intercepts and slopes are interpreted as the expected change in E* associated with each predictor trait. No Choice trial intercepts and slopes are less intuitive to interpret because they are a component of the logit link of the glmm binomial model.

The generalized linear models used for No Choice trait analyses suppose that seed predation has a binomial distribution whose log-odds vary linearly with an independent predictor, in this case a seed trait. The simplified log-odds equation is expressed as:

$$\log\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 X_1$$

Where P is the probability of success (seed is consumed), $1 - P$ is the probability of failure (seed is not consumed), β_0 is the intercept coefficient and β_1 is the coefficient (slope) of the predictor X_1. The log-odds equation can be expressed in terms of probability through the following rearrangement:

$$\frac{P}{1-P} = e^{\beta_0 + \beta_1 X_1} \quad \rightarrow \quad P = \frac{e^{\beta_0 + \beta_1 X_1}}{1 + e^{\beta_0 + \beta_1 X_1}}$$

Unless a value for the X_1 is provided, the intercept and slope coefficients determined by the model can only be interpreted in terms of log-odds. For example, when the slope and intercept are determined, they can be interpreted as a one unit increase in X_1 will result in the increase of β_1 on the log odds of seed predation. The relationship between log-odds and probability is monotonic, so an increase in log-odds translates to an increase in probability. Therefore, if there is a significant positive slope associated with a No Choice trait model, it will be interpreted that an increase in the magnitude of the trait (e.g., greater mass or oil content) will increase the probability of seed predation, which will indicate an increase in seed preference.

RESULTS AND DISCUSSION

Weed seed consumption

Seeds of common weeds species were included in the preference assays to serve as a reference and help us understand how consumption rates compare to

previous studies. In general, weed seed consumption rates in our trials were similar to rates reported from past weed seed preference trials.

No Choice results

Preference patterns for velvetleaf and giant foxtail seeds were consistent with previous research for *H. pensylvanicus.* Lundgren and Rostentrater (2007), White et al. (2007), Ward et al. (2011) and Law and Gallagher, (2015) found velvetleaf was less preferred to giant foxtail. Preference of giant foxtail over common ragweed for *H. pensylvanicus* is also consistent with the literature (Law and Gallagher 2015). No difference was observed in weed seed preference for *P. melanarius* which ate few weed seeds overall. Velvetleaf was the least preferred weed seed for *A. allardi*, but there was no difference in preference between common ragweed and giant foxtail seeds. No difference was observed in weed seed preference for *G. pennsylvanicus*, which may be due to the relatively small number of trials and thus large confidence intervals generated by the model (Nakagawa and Cuthill 2007).

Choice results

Velvetleaf was the least preferred weed species of all ISPs. Although some velvetleaf seeds were eaten in the No Choice trials (up to 5% with *G. pennsylvanicus*), when simultaneously offered seeds from twelve other plant species, ISPs did not eat a single velvetleaf seed. Trends in weed seed preference were consistent for *H. pensylvanicus* and *A. allardi* between No Choice and Choice trials. *P. melanarius* and

G. pennsylvanicus preferred giant foxtail and ragweed seeds over velvetleaf. Low ISP consumption rates of velvetleaf seeds have been attributed to their large size and hard coats (Lundgren and Rosentrater 2007; Ward et al. 2014; Carmona et al. 1999).

Effect of seed type

Cover crop seeds were readily consumed by all ISPs. Seed type (weed or cover crop) had no effect on probability of seed destruction for *H. pensylvanicus* No Choice ($P = 0.20$) and Choice trials ($P = 0.90$), *A. allardi* in No Choice ($P = 0.06$) and Choice trials ($P = 0.16$), and *G. pennsylvanicus* in No Choice ($P = 0.30$) and Choice trials ($P = 0.06$). Interestingly, cover crop seeds were preferred to weed seeds for *P. melanarius* in No Choice ($P < 0.001$) and Choice trials ($P = 0.01$) (Figures 2.3 and 2.4). This indicates that *P. melanarius* could be doing more harm than good in cropping systems. Overall, results support our hypothesis that cover crop seeds would be consumed much as weed seeds by ISPs.

Cover crop seed preference

No Choice results

Four of the ten cover crop species were consistently the least preferred across the four ISPs. Less than 45% of seeds were consumed of barley, hairy vetch, forage radish and white mustard across all ISP. We estimated barley seeds to be relatively soft (Table 2.2), however, a fibrous hull protected the seeds, which might have been difficult for the ISP to chew through. The reason why consumption of hairy vetch seed

was low might be a combination of its large size and hard seed coat. Honek et al. (2003) found a strong relationship between carabid body mass and the average mass of its preferred seeds ($P < 0.001$), three of our ISPs may be too small to adequately feed on hairy vetch. Additionally, we estimated hairy vetch seeds would require 11.92 MPa to break, based on values determined by Rybiñski et al. (2009) for common vetch (*Vicia sativa* L.), a close relative of hairy vetch. This estimate is 42% higher than the estimated MPa required to break velvetleaf seeds (Lundgren and Rosentrater 2007), and may not have been possible for ISPs to overcome. Both forage radish and white mustard are brassicas and produce the defense compounds isothiocynates and glucosinolates, which might deter feeding (Jadoun et al. 2016; Popova et al. 2017) and thus lower ISP preference for them.

Choice results

Cover crop seed preference results from the Choice trials differed slightly from the No Choice trials, indicating the availability of seed from other plant species influences ISP seed preference. Consistent with the No Choice trials, hairy vetch was the least preferred cover crop species by all ISPs. Interestingly, forage radish and white mustard were among the most preferred cover crop species for *P. melanarius* and *G. pennsylvanicus*, respectively, suggesting that a plant species might be undesirable when it is the only species available, but preferred when other species are present. In a similar preference experiment, Honek et al. (2003) found the preference of two carabid species for a reference seed was affected by what other seeds were

offered. Geometric frameworks for nutrition may explain changes in ISP seed preference between No Choice and Choice trials. When only one nutritionally suboptimal food source is available, an insect can feed until it satisfies one of its nutritional requirements while suffering a deficit or excess in another. Alternatively, it can feed to a compromise point where it does not satisfy any of its nutritional requirements, but experiences less extreme nutritional deficits or excesses (Behmer 2009). Forage radish and white mustard may not have been preferred by *P. melanarius* and *G. pennsylvanicus* in No Choice trials because the ISPs were "compromise feeding," but preferred in Choice trials because other seeds could help satisfy nutritional requirements.

Preference of cover crops by individual invertebrate seed predators

Results from both No Choice and Choice trials support our hypothesis that seed predation would vary by ISP and plant species (Figures 2.1 and 2.2). The results also support our hypothesis that seed predation would be driven by morphological and nutritional traits of seeds; however, the relationship between seed traits and consumption varied by ISP and between No Choice and Choice trials (Table 2.4).

H. pensylvanicus consumed 30% of total seeds given in No Choice trials and 20% of total seeds given in Choice trials. *H. pensylvanicus* consumed giant foxtail more than all other plant species, followed by three cover crop species, annual ryegrass, pearl millet, and red clover. Greater seed mass decreased the probability of seed predation in No Choice ($P < 0.001$) and Choice ($P = 0.01$) trials. Greater seed

protein content decreased the probability of seed predation in Choice trials ($P = 0.03$). Other studies have shown that *H. pensylvanicus* prefers small, hard seeds (Lundgren and Rosentrater 2007), especially giant foxtail (White et al. 2007; Ward et al. 2014; DiTomasso et al. 2014).

P. melanarius consumed 13% of total seeds given in No Choice trials and 16% of total seeds given in Choice trials. In No Choice trials, pearl millet was consumed more than twice as much as any other seed species. In Choice trials, there was no difference in preference between pearl millet, forage radish and triticale. Greater seed volume increased the probability of predation in No Choice ($P < 0.001$) and Choice ($P = 0.02$) trials. Greater seed strength decreased the probability of predation in No Choice ($P < 0.001$) and Choice ($P = 0.05$) trials. Greater seed oil ($P < 0.001$) content increased the probability of predation in Choice trials ($P = 0.005$). *P. melanarius* is known as a slug predator (Symondson et al. 1996), but will consume seeds (Fawki et al. 2003) in the spring (Mauchline et al. 2005). Kulkarni et al. (2015b) found *P. melanarius* will consume canola seeds (*Brassica napus* L.). Petit et al. (2014) found *P. melanarius* preferred seeds of shepherd's purse (*Capsella bursa-pastoris* L.) and Canada thistle (*Cirsium arvense* L.) more than common groundsel (*Senecio vulgaris* L.), dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers), and field violet (*Viola arvensis* Murr.). In addition to our results showing that it acted more like a pest than a beneficial organism (i.e. preferred cover crop seeds over weed seeds), it is important that the seed preference of *P. melanarius* be studied further because it is introduced to North America and its range is expanding (Hajek et al. 2008).

A. allardi consumed 21% of total seeds given in No Choice trials and 16% of total seeds given in Choice trials. In No Choice trials, *A. allardi* consumed common ragweed, pearl millet, cereal rye, and triticale with equal preference. In Choice trials, triticale was the most preferred seed species, and common ragweed was rarely consumed. Greater seed volume increased the probability of predation in No Choice ($P < 0.001$) and Choice ($P = 0.001$) trials. Greater seed strength ($P = 0.002$) decreased the probability of predation in No Choice trials. Greater seed mass ($P = 0.01$) and protein ($P = 0.002$) content decreased the probability of predation in Choice trials. Despite being touted as an important seed predator, we are aware of no studies that have evaluated its seed preference (Lundgren 2009). One field study correlated the activity of *A. allardi* with predation of giant foxtail seeds (O'Rourke et al. 2006).

G. pennsylvanicus consumed 61% of total seeds given in No Choice trials and 51% of total seeds given in Choice trials. In the No Choice trials, pearl millet, cereal rye, triticale, and red clover were consumed more than velvetleaf. Greater seed volume increased the probability of predation in No Choice trials ($P < 0.001$), and in Choice trials ($P = 0.04$). Greater seed oil content ($P = 0.03$) and oil to protein ratio ($P = 0.002$) decreased the probability of predation in No Choice trials. To our knowledge, there are few studies that examined seed preference of *G. pennsylvanicus*. Carmona et al. (1999) found that *G. pennsylvanicus* fed on seeds of different size and strength, Lundgren and Rosentrater (2007) determined seed preference to be unrelated to seed traits, and van der Laat et al. (2015) found *G. pennsylvanicus* preferred smaller seeds to larger seeds.

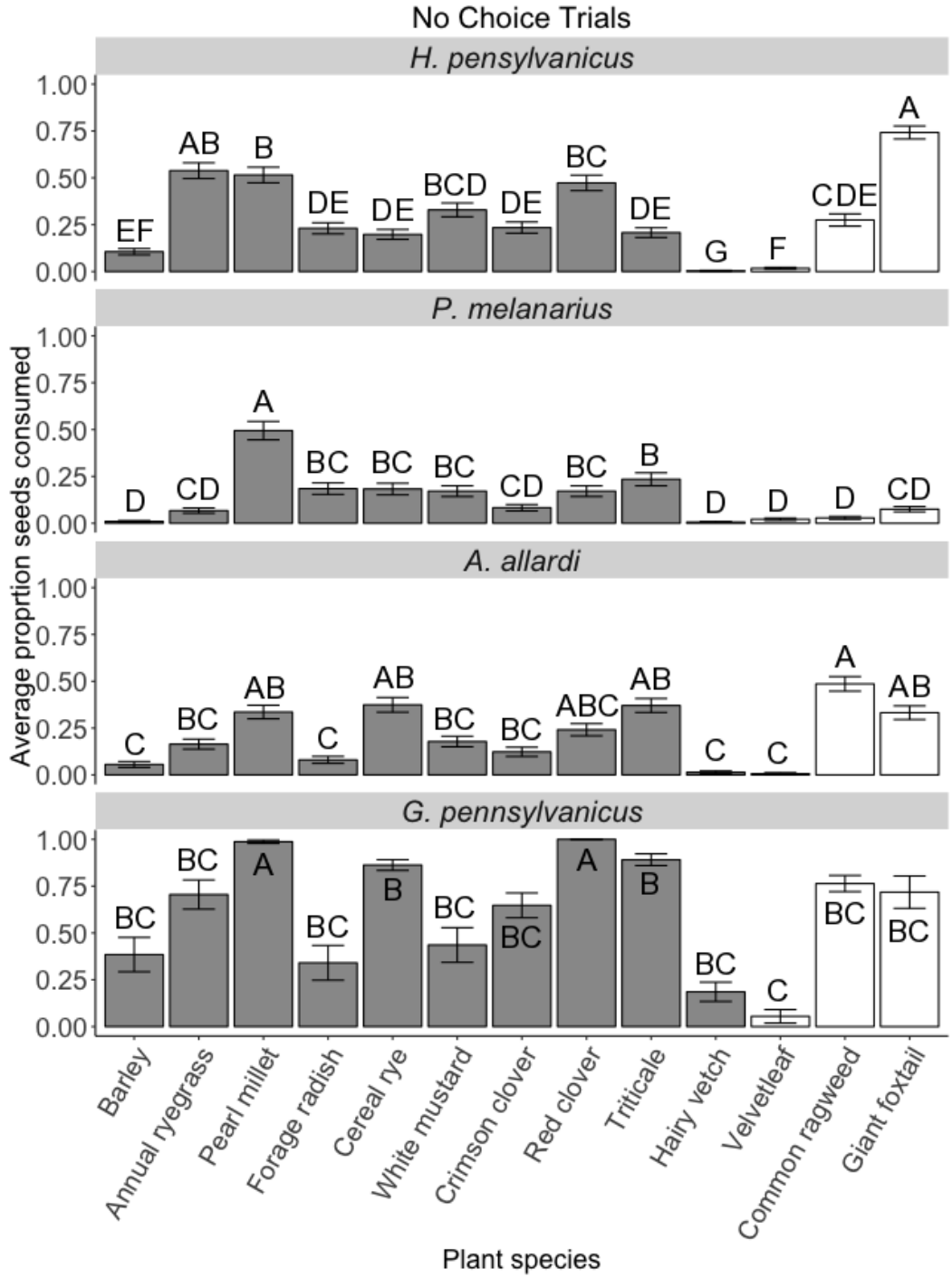

Figure 2.1. Cover crop (grey) and weed (white) seed preference of ISPs in No Choice preference trials. Similar uppercase letters above bars within an ISP panel indicate no significant difference ($P > 0.05$) in preference between plant species.

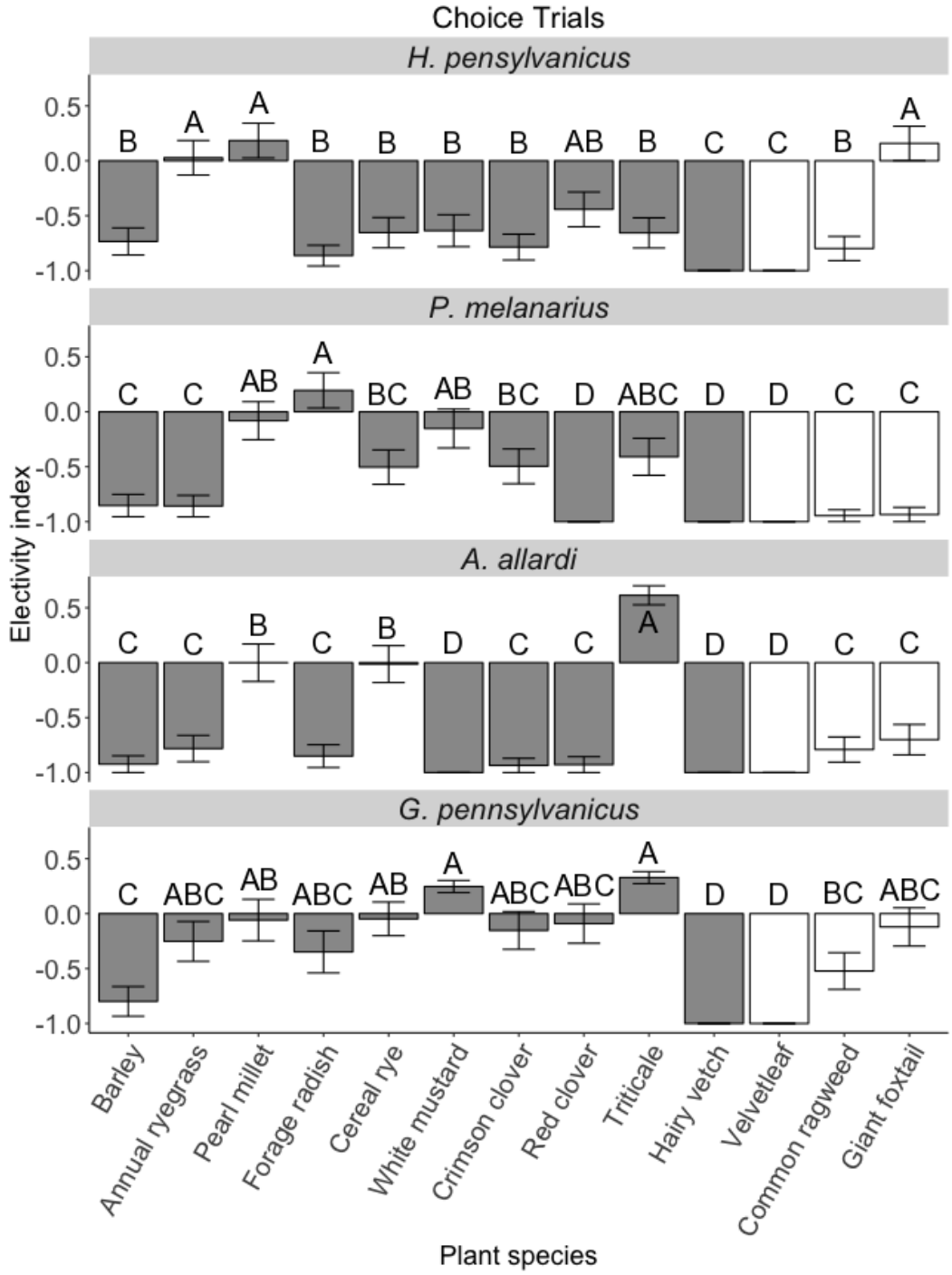

Figure 2.2. Cover crop (grey) and weed (white) seed preference of ISPs in Choice preference trials. The electivity index (E*) is used as a proxy for preference, where a positive value indicates preference and a negative value indicates avoidance. Similar uppercase letters above bars within an ISP panel indicate no significant difference ($P > 0.05$) in preference between plant species.

Table 2.4. Regression equations and associated P-values of the effect of six seed traits on seed predation by four invertebrate seed predators. Oil and protein content were expressed as the proportion of seed weight. O:P is the oil to protein content ratio. Slopes of No Choice equations can be interpreted as the increase or decrease on the log odds of a seed being consumed. Slopes of Choice equations can be interpreted as the increase or decrease in the Vanderploeg and Scavia electivity index (E*) of a seed.

	H. pensylvanicus		*P. melanarius*		*A. allardi*		*G. pennsylvanicus*	
Seed trait	Equation	P	Equation	P	Equation	P	Equation	P
No Choice								
Mass (mg)	**-0.21 - 0.06x**	**<0.001**	-1.97 - 0.005x	0.56	-1.26 - 0.003x	0.71	0.54 - 0.007x	0.71
Volume (mm^3)	-0.94 - 0.003x	0.38	**-2.31 + 0.02x**	**<0.001**	**-1.66 + 0.01x**	**<0.001**	**-0.32 + 0.03x**	**<0.001**
Strength (MPa)	**-0.82 - 0.06x**	**0.08**	**-2.08 - 0.14x**	**<0.001**	**-0.53 - 0.13x**	**0.002**	**0.76 - 0.12x**	**0.10**
Oil content	-0.88 - 0.70x	0.46	**-2.48 + 1.56x**	**0.10**	-1.17 - 1.13x	0.21	**0.89 - 3.54x**	**0.03**
Protein content	-0.61 - 1.15x	0.19	-2.41 + 0.52x	0.67	-0.96 - 1.45x	0.15	0.58 - 0.63x	0.78
O:P	**-0.68 - 0.38x**	**0.08**	-1.90 - 0.006x	0.98	-1.12 - 0.38x	0.13	**1.12 - 1.28x**	**0.002**
Choice								
Mass (mg)	**-0.37 - 0.01x**	**0.01**	-0.69 - 0.005x	0.44	**-0.96 - 0.02x**	**0.01**	-0.38 - 0.004x	0.57
Volume (mm^3)	-0.52 - 0.001x	0.67	**-0.82 + 0.008x**	**0.02**	**-1.07 + 0.02x**	**0.001**	**-0.52 + 0.009x**	**0.04**
Strength (MPa)	-0.72 - 0.006x	0.78	**-0.27 - 0.06x**	**0.05**	-0.74 - 0.02x	0.58	-0.17 - 0.03x	0.39
Oil content	**-0.43 - 1.07x**	**0.06**	**-0.81 + 1.7x**	**0.005**	**-0.49 - 1.23x**	**0.06**	-0.34 - 0.12x	0.88
Protein content	**-0.22 - 1.48x**	**0.03**	-0.76 + 0.66x	0.43	**-0.15 - 2.22x**	**0.002**	-0.40 + 0.32x	0.74
O:P	**-0.41 - 0.27x**	**0.06**	-0.75 + 0.26x	0.14	-0.50 - 0.29x	0.11	-0.25 - 0.15x	0.46

Effect of invertebrate seed predator on seed consumption by plant species

ISPs did not consume or consumed very little hairy vetch and velvetleaf seed (Figure 2.3 and 2.4). Seed consumption by ISPs varied for all other species in the No Choice trials. *G. pennsylvanicus* consumed more seeds than the other three ISP for barley, pearl millet, cereal rye, crimson clover, red clover, triticale, and common ragweed. Seed consumption by *H. pensylvanicus* did not differ from *G. pennsylvanicus* for annual ryegrass or giant foxtail, and they both consumed more seed than *P. melanarius* and *A. allardi* for these two plant species. E* by ISPs was the same for common ragweed, barley and pearl millet, but varied for all other species in Choice trials. E* did not differ between *G. pennsylvanicus* and *A. allardi* for triticale, which they both preferred more than either *H. pensylvanicus* or *P. melanarius*. E* did not differ between *G. pennsylvanicus* and *H. pensylvanicus* for giant foxtail and red clover, which they both preferred more than either *P. melanarius* or *A. allardi.* E* did not differ between *G. pennsylvanicus* and *P. melanarius* for white mustard, which they both preferred more than *H. pensylvanicus* or *A. allardi*.

Differences in seed preference between ISPs can probably be explained by ISP mouthpart strength, size, and feeding ecology. Members of the *Harpalus* genus have relatively large mandibular adductor muscles (Evans and Forsythe 1985) and strong mandibles (Acorn and Ball 1991), which likely enable *H. pensylvanicus* to easily destroy and consume small hard seeds (Lundgren and Rosentrater 2007). *G. pennsylvanicus* generally consumed more seeds than the other ISPs, possibly because of its relatively large size and higher caloric intake requirements compared to the other ISPs. Moreover, *G. pennsylvanicus* is an aggressive and territorial species that has

evolved powerful mouthparts for fighting (Jang et al. 2008, Judge and Bonanno 2008), which may also be excellent tools for seed destruction. The relatively lower predation and preference patterns of *P. melanarius* and *A. allardi* may be due to their feeding ecology. Both species are known for consuming other invertebrates and plant material (e.g., Lundgren and Harwood 2012; Jacobs et al. 1992; Allen and Hagley 1990), so their mouthparts may not be suited to feeding exclusively on seeds.

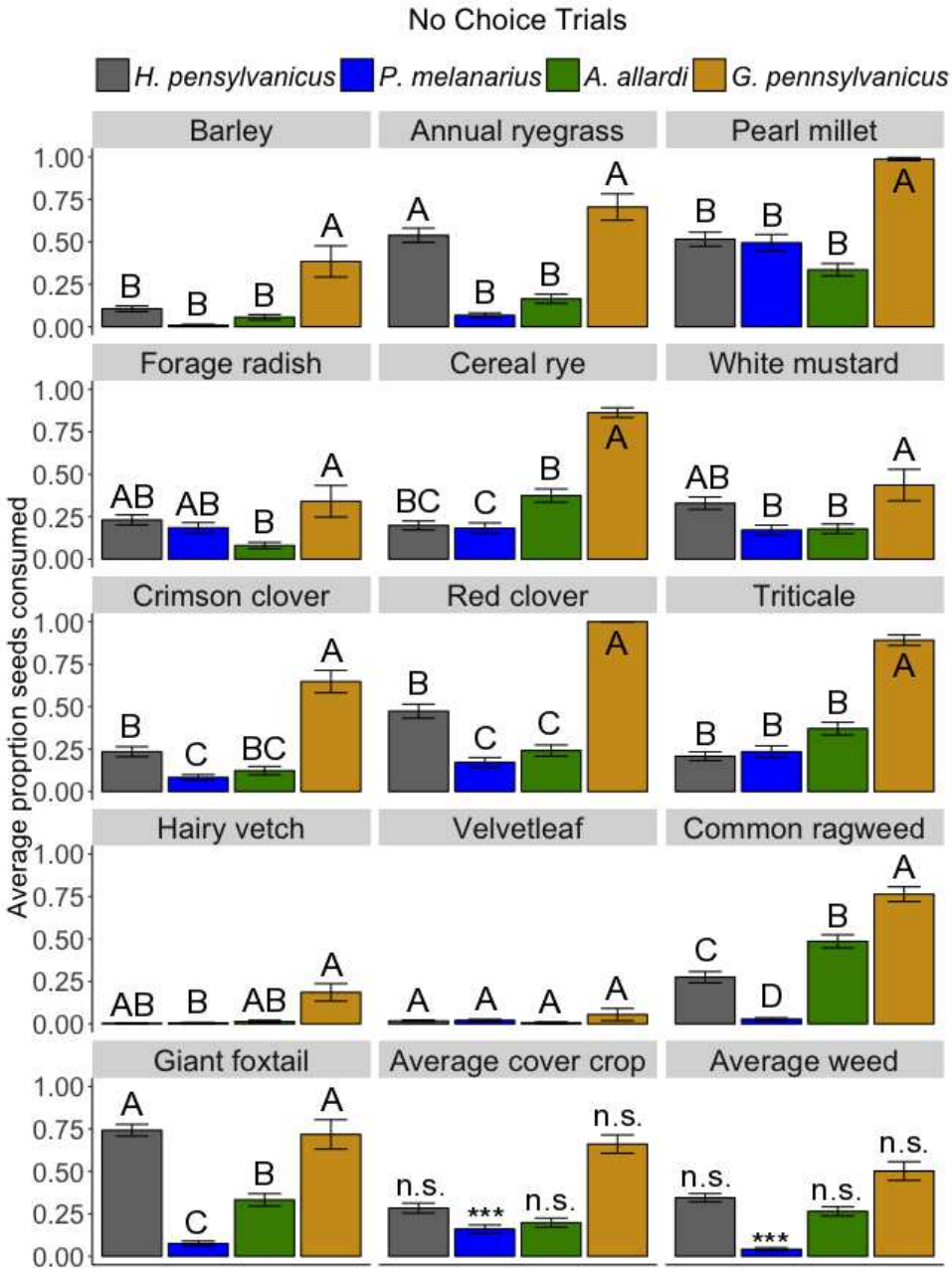

Figure 2.3. Seed preference of ISPs in No Choice preference trials. Similar uppercase letters above bars within plant species panels indicate no significant difference ($P > 0.05$) between ISPs for each plant species. Average cover crop and weed panels are the average seed predation rates of each ISP; n.s. means no significant difference of average predation rates between cover crops and weeds within each ISP ***means a significant difference ($P < 0.001$).

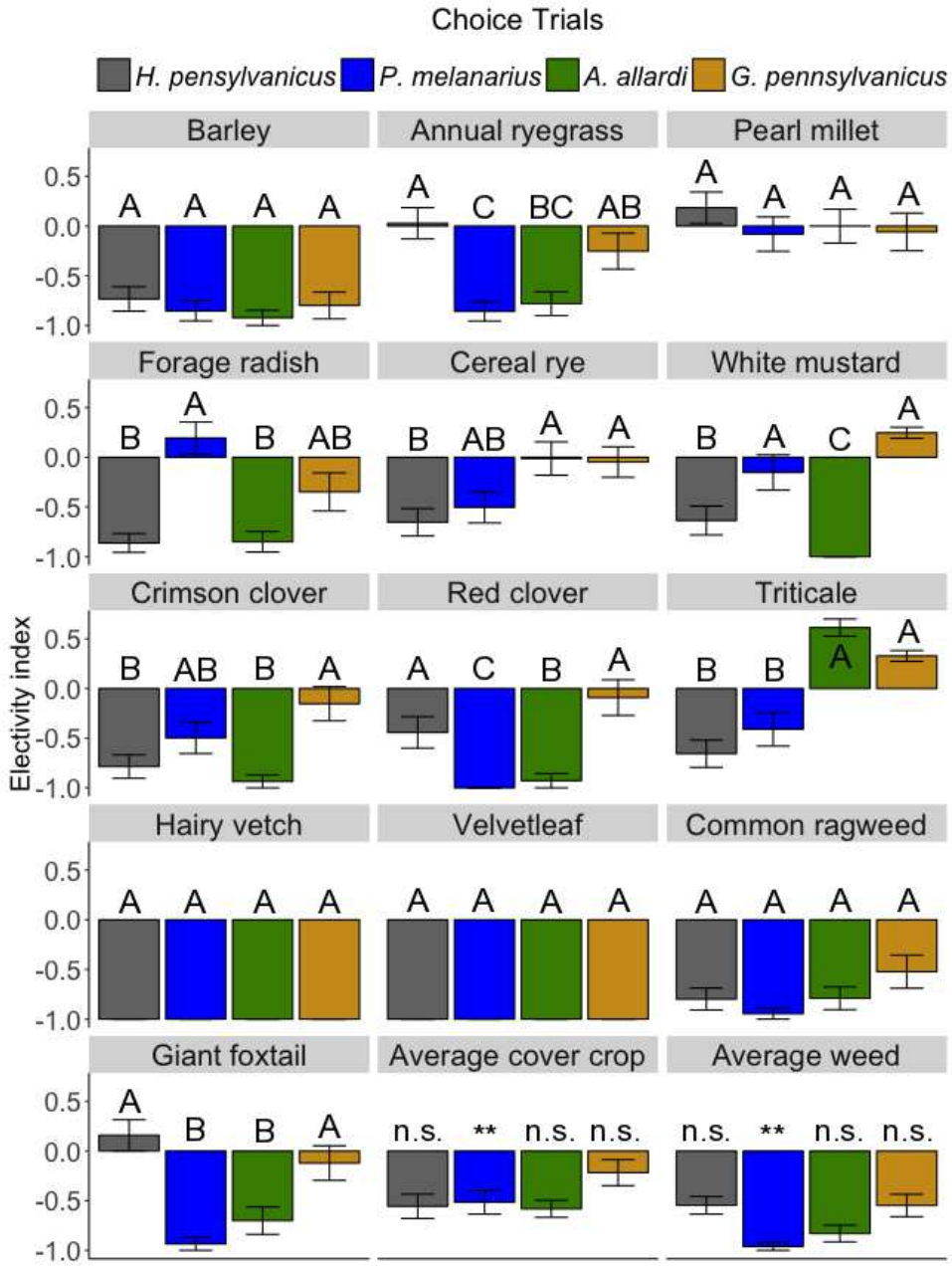

Figure 2.4. Seed preference of ISPs in Choice preference trials. Similar uppercase letters above bars within plant species panels indicate no significant difference (P > 0.05) between ISPs for each plant species. The electivity index (E*) is used as a proxy for preference, where a positive value indicates preference and a negative value indicates avoidance. Average cover crop and weed panels are the average E* of each ISP; n.s. means no significant difference of average predation rates between cover crops and weeds within each ISP **means a significant difference (P = 0.01).

Experiment considerations

In our research we offered ISPs 26 seeds regardless of seed size or volume. Although we standardized the number of seeds, we also could have standardized the mass of seeds or the volume of seeds offered to ISP. Most ISP seed preference research has used the total seed biomass consumed to establish preference (e.g., Honek et al. 2006; Lundgren and Rosentrater 2007; Ward et al. 2014), but this metric is not used exclusively (e.g., Petit et al. 2014; Carmona et al. 1999). In our research, we used the number of seeds destroyed instead of total seed biomass consumed because it simplified the experimental process. It was noted that all insects focused their feeding near the seed embryo, and rarely consumed a whole seed before consuming a new one. Analyzing the number of seeds damaged to the point of non-germination, such as what we have done, is likely to be more applicable to farmers who are interested in reducing weed populations.

In previous seed preference research, trials have often been conducted using imbibed or wetted seeds. Dry seeds were used in our experiment because it better reflects seed conditions immediately following weed seed shed and broadcast seeding for cover crops. It is unclear if using dry seeds versus imbibed seeds will alter ISP seed preference. Research on the material properties of seeds (e.g., Babic et al. 2011; Bargale and Irudayaraj 1995) consistently shows that the force required to break a seed decreases with increased moisture content. If seed predation is determined by the force required to break a seed, then preference should change when hard, unpalatable, seeds have high moisture content. However, Law and Gallagher (2015) showed *H. pensylvanicus* preference trends between imbibed and dry seeds were not different.

Management Implications

Although ISPs play an important role in limiting weed populations, the results from this research show that they can also be pests and consume seeds of commonly grown cover crop species. All four ISP species that we tested readily consumed cover crops seeds in both No Choice and Choice preference trials. These four species are active seed predators from at early summer through autumn in the study region (O'Rourke et al. 2006; Hajek et al. 2007; Lundgren 2009; Ward et al. 2014. This timing coincides with the period in which farmers seed cover crops. Thus ISPs are likely having a large, but understudied, effect on limiting cover crop establishment, especially when seeds are left on the soil surface. However, it is important to keep in mind that other granivores such as birds and mice can also a large effect on cover crop establishment based on field trials showing greater predation in open compared caged seed cards that exclude vertebrates (Youngerman et al. 2015).

Farmers and seed companies can use the results of our research for cover crop species selection, and choose species that are less likely to be consumed by ISPs for broadcast seeding. Based on our findings showing which cover crops are the least palatable to ISP, we recommend farmers consider the possibility of cover crop seed predation, and select hairy vetch and barley if they are concerned about seed losses to ISPs. However, large seeded species such as hairy vetch and barely generally do not establish as well as small seeded species when sown by broadcasting. Cover crop plant breeders are selecting for smaller seed size in new varieties of cover crops. While this may be better for broadcasting, smaller seeds may be more palatable to ISPs (Lundgren and Rosentrater 2007; White et al. 2007; Ward et al. 2014). Additionally,

farmers should be encouraged to bury cover crop seed by using a drill that makes a furrow, deposits the seed, and then covers it with soil.

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APPENDIX

Effect of corn density on corn grain yield within each site and Effects of crop density treatments across sites

In the sections listed above, it was helpful to have site-wide means of corn grain yields, corn density and cover crop and weed biomass from both dates. Least squared means were calculated for each variable and compared between sites with the cld function (package lsmeans). These means allowed for quick comparisons between sites, but did not expand the discussion because we were interested in 1) determining differences at the treatment*site*time level; or 2) determining linear relationships between the variables. The grain yield data was used to compare with county-wide averages.

Table Y. Lsmeans comparisons of linear mixed effects models for the mean value across all treatments for variables at each site. CD is corn density, ACCB is log-transformed August cover crop biomass, OCCB is log-transformed October cover crop biomass, AWB is log-transformed August weed biomass, OWB is log-transformed October weed biomass. LCI is the lower confidence interval, UCI is upper confidence interval. Similar letters next to means within a column indicate no significant difference ($\alpha = 0.05$).

Variable	Units	Site	LSmean	LCI	UCI	Group
Yield	g/m^2	NY	1051	980.3	1121.8	A
		PA	703	635.7	770.5	B
		MD	735	667.4	802.2	B
CD	$plants/m^2$	NY	4.9	3.6	6.3	A
		PA	3.9	2.6	5.3	A
		MD	5	3.7	6.4	A
ACCB	g/m^2	NY	2.1	1.5	2.7	A
		PA	2	1.4	2.7	A
		MD	1.8	1.2	2.3	A
OCCB	g/m^2	NY	3	2.3	3.7	A
		PA	2.8	2.1	3.5	A
		MD	2.1	1.4	2.8	A
AWB	g/m^2	NY	0.49	-0.2	1.2	A
		PA	4.6	3.9	5.3	C
		MD	3.2	2.5	3.9	B
OWB	g/m^2	NY	0.9	0.2	1.6	A
		PA	4.2	3.5	4.9	B
		MD	3	2.4	3.7	B

APPENDIX 2

Survival

A univariate survival analysis (package survival) was used to determine if the within insect species death curves were different between seed species. A second univariate survival analysis was used to determine if average survival rate was the same for all ISPs. Survival data was taken from No Choice trials, and a binary censor variable was added to the dataset for individuals who lived past through the entire experiment. Statistically significant differences ($P \leq 0.05$) between survival curves was analyzed using the Kaplan-Meier test, with rho = 0 (package survminer). This test is a common non-parametric log-rank test for survival analysis (Bretz et al. 2011).

Survival analysis showed no significant difference between the survival curves of seed species for any of the insects (*A. allardi*: $X^2 = 18$, df = 12, P = 0.11; *G. pennsylvanicus*: $X^2 = 16.4$, df = 12, P = 0.17; *H. pensylvanicus*: $X^2 = 9.6$, df = 12, P = 0.65; *P. melanarius*: $X^2 = 15.1$, df = 12, P = 0.23). The mean survival curve between ISP species was significantly different ($X^2 = 10.5$, df = 3, P = 0.01).

It is possible that the relatively small sample size and large number of groups (seeds species) caused the survival analysis to have low power (Moore 2016). Unfortunately, it is hard to find an appropriate test for power when comparing more than two groups in survival analysis (Qui et al. 2009). There no significant difference between survival curves for any ISP No Choice trials, so death was unrelated to whether the insect had consumed any seeds. In other words, ISPs were dying at the same rate across all seed species. Survival analysis may have implications for interpreting seed preference in No Choice trials.

For example, *A. allardi* consumed around 50% of common ragweed seeds in No Choice trials, but its probability of survival was no different from trials where it consumed almost no seeds (e.g., velvetleaf). So even though *A. allardi* consumed lots of common ragweed seeds, it may not have been getting the required nutrition to live. Therefore common ragweed preference in the No Choice trials may not be an accurate representation of the true seed preference of *A. allardi*. This point is underscored in that *A. allardi* did not prefer common ragweed in Choice trials.

The number of deaths as a percent of total insects was 3 times greater in No Choice trials than Choice trials. It is likely that the diversity of seeds presented in the Choice trials provided a full spectrum of nutrients more reflective of field conditions. Choice trial preference results could therefore be more indicative of an insect's actual seed preference. Mean survival probability was highest for *G. pennsylvanicus* and *H. pensylvanicus.* This result in and of itself is not useful. However, if survival rates are tracked in future studies, it could be determined which factors (e.g., starvation time) affect insect death, and an experimental design which optimizes survival could be developed.